THE GENERA OF HOLARCTIC ELAPHRINI AND SPECIES OF *ELAPHRUS* FABRICIUS (COLEOPTERA: CARABIDAE): CLASSIFICATION, PHYLOGENY AND ZOOGEOGRAPHY.[1]

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ABSTRACT

*The tribe, genera, and subgenera of Elaphrini are redefined on characters of adults and larvae. Recognized are three genera of Elaphrini, (*Diacheila *Motschulsky,* Blethisa *Bonelli, and* Elaphrus *Fabricius), four subgenera of* Elaphrus *Fabricius, (*Arctelaphrus *Semenov,* Neoelaphrus *Hatch,* Elaphrus, *and* Elaphroterus *Semenov), 34 species and 3 subspecies of* Elaphrus. *Keys to genera of Elaphrini and to subgenera, species and subspecies of* Elaphrus *are given for adults and known larvae.*

Four species are described as new: E. lindrothi *(type locality: United States: Illinois, Jackson Co., 3 mi. N. Pomona),* E. marginicollis *(type locality: United States: Colorado, Jack's Gulch, Roosevelt N.F.),* E. mimus *(type locality: United States: California, Angwin), and* E. comatus *(type locality: China, Heilung Kiang, Harbin). The following synonymies are proposed for the first time:* Elaphrotatus *Semenov 1895* = Elaphroterus *Semenov 1895;* Elaphrus ruscarius foveatus *Pierce 1948* = Elaphrus finitimus *Casey 1920;* Elaphrus clairvillei lynni *Pierce 1948* = Elaphrus clairvillei *Kirby 1837.*

Treatment of each species includes: synonymic list, diagnostic combination and description of adults and larvae, discussion of variation, derivation of the specific epithet, geographic distribution, collecting notes, taxonomic notes, and geographical affinities. Important character states are illustrated. Geographical distributions are mapped for all North American species of Elaphrus . *Results of statistical analyses of geographic variation of each species are discussed.*

Relationships of genera and subgenera of Elaphrini are established using separate procedures of phenetic and cladistic systematics, based independently on characters of adults and larvae. A phylogeny is reconstructed for genera of Elaphrini, and for subgenera and species of Elaphrus *based on structural characters of adults and larvae.*

It is postulated that the ancestral elaphrine stock evolved and radiated in tropical Asia where it became extinct except for the immediate ancestor of the elaphrines surviving in the temperate zone of northernmost Siberia and Alaska in the Late Cretaceous. There, it radiated and gave rise to ancestors of extant genera and subgenera. The history of elaphrine evolution is a succession whereby ancestral peripheral elements extend into areas of low diversity followed by radiation. This pattern was repeated with the formation of the cold temperate,

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[1]Modified and expanded from a thesis submitted to the University of Alberta in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

boreal and arctic zones.

RÉSUMÉ

*A l'aide des caractères morphologiques de l'adulte et de la larve, la tribu, genres et sous-genres des Elaphrini sont définis de nouveau. Nous reconnaissons trois genres à l'intérieur de la tribu (*Diacheila *Motschulskay,* Blethisa *Bonelli et* Elaphrus *Fabricius), quatre sous-genres à l'intérieur du genre* Elaphrus *(*Arctelaphrus *Semenov,* Neoelaphrus *Hatch,* Elaphrus, *et* Elaphroterus *Semenov), ainsi que 34 espèces et 3 sous-espèces du genre* Elaphrus. *Nous présentons des clefs de détermination pour les adultes et larves connues des genres d'Elaphrini, ainsi que des sous-genres, espèces et sous-espèces d'*Elaphrus.

Quatre nouvelles espèces pour la science sont décrites: E. lindrothi *(localité-type: Etats Unis: Illinois, Comté de Jackson, 5 km au nord de Pomona)* E. marginicollis *localité-type: Etats Unis: Colorado, Jack's Gulch, Forêt Nationale de Roosevelt),* E. mimus *(localité-type; Etats Unis: Californie, Angwin), et* E. comatus *(localité-type: Chine: Heilung Kiang, Harbin). Les synonymes suivants sont proposés pour la première fois:* Elaphrotatus *Semenov 1895* = Elaphroterus *Semenov 1895;* Elaphrus ruscarius foveatus *Pierce 1948* = Elaphrus finitimus *Casey 1920;* Elapharus clairvillei lynni *Pierce 1948* = Elaphrus clairvillei *Kirby 1837. Pour chaque espèce traitée dans ce travail, les informations suivantes sont incluses: liste des synonymes, diagnose et description de l'adulte et de la larve, discussion de la variation géographique, origine des noms nouveaux proposés, répartition géographique, notes sur l'habitat et la biologie, notes taxonomiques et affinités géographiques. Les caractères morphologiques importants sont illustrés de même que la répartition géographique des espèces néarctiques du genre* Elaphrus. *Les résultats de l'analyse statistique de la variation géographique de chaque espèce sont également discutés.*

*Les relations d'affinité entre les genres et sous-genres d'Elaphrini ont été établies à partir des techniques phénétiques et cladistiques, basées indépendamment sur les caractères morphologiques de l'adulte et de la larve. Nous présentons également un arbre phylogénétique des genres d'Elaphrini et des sous-genres et espèces d'*Elaphrus *établi à l'aide des caractères de l'adulte et de la larve.*

Nous croyons que la lignée ancestrale des Elaphrini s'est développée et répandue en Asie tropicale pour ensuite y disparaître sauf pour l'ancêtre immédiat des Elaphrini qui a probablement survécu dans les régions tempérées de la Sibérie septentrionale et de l'Alaska à la fin du Crétacé. Cet ancêtre par la suite à évolué dans cette région et donné naissance aux lignées ancestrales des genres et sous-genres actuels. L'histoire évolutive des Elaphrini est perçue comme une sussession d'invasions d'éléments périphériques vers des régions de faible diversité suivie de spéciation. Ce patron s'est répété lors de la formation des régions tempérées, boréales et arctiques.

TABLE OF CONTENTS

INTRODUCTION

Since capturing my first specimen of *Elaphrus* in 1962, I have remained excited by these beetles. Adults of most species are beautifully sculptured, and some are brilliantly coloured. Moreover, the marked specialization in habitat requirements of many species fascinated me (Goulet, 1964).

Adults of *Elaphrus* are easy to recognize because of their cicindeloid shape, and four rows of large elytral depressions (pits). Unfortunately many species of the subgenus *Elaphrus* are difficult to characterize. However, Lindroth, (1961) in his revision of North American species, laid the groundwork for further studies.

This work is intended as a continuation of Lindroth's work. I deal with intraspecific variation, larvae, behaviour, and habitat requirements. Although I focus much of my efforts on North American species, I include all Palaearctic taxa known to me. I gathered large amounts of structural evidence about adults and larvae to test separate phylogenetic reconstructions for congruence, and to help students of fossil insects working with fragments of specimens. More detailed descriptions are in my thesis (1978, University of Alberta, Edmonton, Canada). Finally, I attempt to trace past zoogeographical events.

Cicindela riparia Linnaeus , 1758, was the first formally recognized species of *Elaphrus*. Fabricius (1775) erected the genus *Elaphrus* to include the above species, and others that are today in *Notiophilus* Duméril, 1806, and *Bembidion* Latreille, 1802. Latreille (1810) designated *E. riparius* as type species, and excluded *Bembidion* from *Elaphrus*. Dejean (1826) published the first revision and restricted *Elaphrus* to its present concept. Some authors after Dejean used the genus *Elaphrus* in a wider sense: Brullé(1834) included *Pelophila* Dejean, 1828, and *Blethisa* Bonelli, 1810; Lacordaire (1854) added *Opisthius* Kirby, 1837. However, Dejean's concept became generally accepted.

Semonov (1895, 1926), who was studying the rich Russian *Elaphrus* fauna, recognized the natural species-groups of *Elaphrus,* and arranged the species in five subgenera.

Larvae were first described by Schiødte (1867). Major advances in knowledge of larvae were made by van Emden (1919, 1942), Lindroth (1954) and Luff (1976). Presently all elaphrine genera and subgenera can be recognized in larval stages.

In a few recent works, precise habitats of many species were described (Lindroth, 1949, 1961). Bauer (1973, 1974 and 1976) provided much insight about behaviour, ecological relationships and dispersal potential of some species of *Elaphrus*.

I hope that my work will not only make possible indentification of specimens, but also stimulate more detailed investigations into the many problems in evolutionary biology that render members of this genus so interesting. Thus, I have attempted to solve some of the many problems in speciation of North American *Elaphrus,* to improve classification of the Palaearctic *Elaphrus* complex, and to point out many other problems that demand particular

attention.

MATERIALS AND METHODS

Materials

I based this study on about 18,000 adults (1500 Palaearctic) and 400 larvae (20 Palaearctic). Most adults were loaned to me by various institutions and private collectors in Canada, United States and Europe. Larval material came mostly from my collection (all *ex ovo,* C.H. Lindroth (Sweden) and T. Bauer (Austria). Fossil fragments from Pleistocene and Miocene deposits were provided by J.M. Matthews, A.A. Morgan, A. Ashworth and R.E. Morlan. The following abbreviations, mostly from Arnett (1969), represented these collections and their respective curators.

ALAR A. Larochelle, Collège Bourget, C.P. 1000, Rigaud, Québec. J0P 1P0.

AMNH Department of Entomology Collection, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024; L.H. Herman.

ANSP Department of Entomology Collection, Academy of Natural Sciences, 19th and Parkway, Philadelphia, Pennsylvania 19103; M.G. Emsley.

BMCS Musée d 'Histoire Naturelle de Bale, Bale, Suisse; W. Whittmer.

BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW.7 5BD, England; R. Aldridge.

BMSC Buffalo Museum of Science, Humbolt Park, Buffalo, New York 14211; H.W. Charnley.

BMUW Burke Museum, Department of Zoology, University of Washington, Seattle, Washington 98105; M.H. Hatch.

CASC Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; D.H. Kavanaugh.

CDAE Bureau of Entomology, State of California, Department of Agriculture, 1220, N. St., Sacramento, California 95814; T. N. Seeno.

CISC California Insect Survey, Division of Entomology and Acarology, University of California, Berkeley, California 94720; J.A. Chemsak.

CJEA C. Jeanne, Bordeaux, France.

CNCI Canadian National Collection of Insects, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario K1A 0C6; A. Smetana.

CSLB Entomological Collections, California State College at Long Beach, Long Beach, California 90801; E.L. Sleeper.

CUIC Cornell University Insect collection, Department of Entomology, Cornell University, Ithaca, New York 14850; L.L. Pechuman.

CWSC Canadian Wildlife Service Collection, Ottawa, Ontario K1A 1C7; R.I.G. Morrison.

DEFW Department of Entomology, Fisheries and Wildlife Collection, University of Minnesota, St. Paul, Minnesota 55101; P.J. Clausen.

DEUN Department of Entomology Collection, University of Nebraska, Lincoln, Nebraska 68503; B.C. Ratcliffe.

DHKA D.H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

DMNH Dayton Museum of Natural History, 2629 Ridge Ave., Dayton, Ohio 45414; E. J. Koestner.

DRWH D.R. Whitehead, Agriculture Research Service, c/o United States National Museum, Washington, District of Columbia 20560.

DZEC Department of Zoology and Entomology Collection, Montana State University, Bozeman, Montana 59715; N.L. Anderson.

EJKC E.J. Kiteley, 16-13th Street, Roxboro 900, Québec.

EMUS Entomology Museum, Department of Zoology, Utah State University, Logan, Utah 84321; W.J. Hanson.

ESUW Entomology Section Museum, Plant Sciences Division, University of Wyoming, Laramie, Wyoming 83070; R.J. Lavigne.

FGAC F.G. Andrews, Department of Food and Agriculture, 1220 N. Street, Sacramento, California 95814.

FMNH Division of Entomology Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605; H.S. Dybas.

FNYC F.N. Young, Department of Zoology, Indiana University, Bloomington, Indiana 47401.

FRLC Forest Research Laboratory Collection, Box 4000. Fredericton, New Brunswick; E3B 5P7; G.R. Underwood.

HGOU H. Goulet, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario K1A 0C6.

HHCC H. Hacker, 235 Randall St., San Franscisco, California 94131.

ICCM Section of Insects and Spiders, Carnegie Museum, Pittsburgh, Pennsylvania 15213; G.E. Wallace.

INHS Insect Collection, Illinois State Natural History Survey, Urbana, Illinois 61803; M.W. Sanderson.

ISUI Department of Zoology and Entomology Collection, Iowa State University, Ames, Iowa 50010; J.L. Laffoon.

JBEL J. Belicek, Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3.

JMCI J.M. Cicero, 13641, Terrace Bella St., Pacoima, California 91331.

JSCC Joe Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.

JVMA J.V. Matthews, Jr., Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario K1A 0E8.

KSUC Department of Entomology Collection, Kansas State University, Manhattan, Kansas 66502; H.D. Blocker.

LACM Insect Collection, Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007; C.L. Houes.

LSUC Department of Entomology Collection. Louisiana State University. Baton Rouge, Louisiana 70803; J.B. Chapin.

MCPM Milwaukee City Public Museum, 800 West Wells St., Milwaukee, Wisconsin 53233; K.W. MacArthur, G.R. Noonan.

MCZC Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J.L. Lawrence.

MSUC Department of Entomology Collection, Michigan State University, East Lansing, Michigan 48823; E.R. Hoebeke.

NCSU Department of Entomology Collection, North Carolina State University, Raleigh, North Carolina 27607; D.A. Young.

NDSU Entomology Department Collection, North Dakota State University, Fargo, North Dakota 58102; R.L. Post.

NMDC N.M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.

NSMC Insect Collection, Nova Scotia Museum, Halifax, Nova Scotia B3H 3A6; L. Martin.

OSEC Department of Entomology Collection, Oklahoma State University, Stillwater, Oklahoma 74074; W.A. Drew.

OSUC Ohio State University Collection of Insects and Spiders, 1735 Neil Ave., Columbus, Ohio 43210; C.A. Triplehorn.

PADA Insect Collection, Bureau of Plant Industry, Pennsylvania Department of Agriculture, 2301 North Cameron St., Harrisburg, Pennsylvania 17120; T.J. Henry.

PMNH Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; K.W. Brown.

PSUC Department of Entomology Collection, Pennsylvania State University, University Park, Pennsylvania 16802; K.C. Kim.

PURC Entomology Research Collection, Department of Entomology, Purdue University, Lafayette, Indiana 47907; A. Provonsha.

RFCC R. Freitag, Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1.

ROMC Royal Ontario Museum, University of Toronto, Toronto 5, Ontario M5S 2C6; G.B. Wiggins.

SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044; P.D. Ashlock.

SFAC Department of Biology Collection, Stephen F. Austin State College, Nacogdoches, Texas 75961; W.W. Gibson.

TBAU T. Bauer, I. Zoologisches Institut der Universität Wien, Austria.

UADE Department of Entomology Collection, University of Arkansas, Fayetteville, Arkansas 72701; E.P. Rouse.

UASM Department of Entomology, Strickland Museum, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.

UBCZ Spencer Entomology Museum, Department of Zoology, University of British Columbia, Vancouver 8, British Columbia V6T 1W5; G.G.E. Scudder.

UCDC Department of Entomology Collection, University of California, Davis, California 95616; R.O. Schuster.

UCEC Department of Entomology Collection, University of Colorado, Boulder, Colorado 80302; U.N. Lanham.

UCRC Department of Entomology Collection, University of California, Riverside, California 92502; S.I. Frommer.

UICM Department of Entomology Collection, University of Idaho, Moscow, Idaho 83843; W.F. Barr.

ULIC Department of Biology Insect Collection, University of Louisville, Louisville, Kentucky 40208; C.V. Covell.

UMMZ Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104; R.S. Alexander.

UMRM Entomology Research Museum, 1-87 Agriculture Building, University of Missouri, Columbia, Missouri 65201; W.R. Enns.

USNM Division of Coleoptera, Department of Entomology, United States National Museum of Natural History, Washington, District of Columbia 20560; P.J. Spangler.

UVCC Department of Zoology Collection, University of Vermont, Burlington, Vermont 95401; R.T. Bell.

UWOC Department of Zoology Collection, University of Western Ontario, London Ontario N6A 5B7; W.W. Judd.

UWEM Entomology Museum, Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706; W.J. Bayer.

UMKC V.M. Kirk, Northern Grain Insect Research Laboratory, Brookings, South Dakota 57006.

UZMF Universitetes Zoologiska Museum, Entomologiska Avdelningen, N. Jarnvagsgatan 13, SF-00100 Helsingfors 10, Finland; H. Silfverberg.

WSUC Department of Entomology Collection, Washington State University, Pullman, Washington 99163; M.T. James.

ZMLS Zoological Institute, Department of Systematics, University of Lund, Lund, Sweden; C.H. Lindroth.

Methods

Collection of Specimens.— Adults of all species of *Elaphrus* live along rivers, small streams, swamps, sloughs, or bogs. On substrates of rough organic texture, beetles were taken by treading the vegetation under water. On substrates of fine texture (clay, fine muds), treading was done slowly and gently moving in one direction to force the bettles out of cracks before being trod upon and buried (in cloudy or rainy weather, I do not tread as most beetles of these habitats are inactive then and so will be buried).

In moist but not soggy bogs, where the vegetation could not be trod under water, pitfall traps were most productive. I used pitfall traps successfully in all habitats where *Elaphrus* live. In wet habitats, I used a modified pitfall trap requiring no digging. This trap consists of a 25 cm trough with a gentle sloping ramp allowing beetles to climb up to the trap edge. The latter is rounded rather than sharp to increase efficiency of the trap.

Larvae live in the same habitat as that of adults, but different procedures were used to collect them. Some larvae enter pitfall traps, but a more fruitful method was to gently press by hand the organic surface many times at the same spot. This yielded numerous larvae especially those of the first instar. On fine textured soil or inorganic habitats, repeated splashings with water yielded larvae.

Preservation and preparation.— Adults were killed and stored in ethyl acetate fumes, or were killed and preserved in 70% ethanol (voucher specimens for reared larvae and for dissection). After cleaning, the specimens were mounted on points. Larvae were killed in almost boiling water (heat destroys autolytic enzymes and fixes, after three to five minutes, the body in a straight position) and stored in 70% ethanol, or were killed and stored in 70% ethanol. After cleaning, some larvae were dehydrated (freeze-, critical point-, or chemical-drying) and others were mounted in glycerine so that body proportions were preserved, and the specimen could be

studied and moved easily and viewed from different angles. An efficient glycerine mount can be achieved as follows:

1. If a preserved larva is 5 to 10 mm long, pierce the thorax ventrally or laterally. If larger (10 to 20 mm) pierce the abdomen and enlarge the opening. This facilitates the next step.
2. Place the larva in gently boiling 10% K0H for 3 to 5 minutes.
3. Transfer the larva into distilled water with a wide mouthed eye-dropper to avoid collapsing the body. Neutralize the remnants of K0H by changing most of the water several times.
4. Transfer the larva with wide mouthed eye-dropper into 4% glycerin-water solution (V/V). The best receptacles are concave at the bottom.
5. Place the receptacle on a microscope slide drying plate where water will evaporate (60°C). Add more of the glycerin solution after a few hours. Twelve hours or less is enough to complete the glycerin concentration and impregnation process. The larvae are then ready to be transferred to a ringed slide for study, or to closed vials of glycerin for storage. If larvae are studied at magnifications below 200X, it is not necessary to use cover slips if glycerin is levelled with upper edge of the ring. This greatly facilitates positioning of specimens. The ring should be made of a material that is chemically stable, or the larvae should be on the slide for less than a month.

Rearing of Larvae

Techniques for rearing elaphrines as well as other carabids were previously described (Goulet, 1976). Larvae of most North American *Elaphrus* were reared from eggs (except *E. lapponicus* Gyllenhal, *E. marginicollis* new species, *E. mimus* new species, *E. viridis* Horn and *E. parviceps* Van Dyke). Larvae of last four species are not known, but those of *E. lapponicus* were recognized by association with adults (Lindroth, 1954). In addition, I studied larvae reared from eggs of four palaearctic species (*E. cupreus* Duftschmid, *E. riparius* (Linnaeus), *E. aureus* Müller, and *E. ulrichi* Redtenbacher). I reared from eggs larvea of *Diacheila polita* Faldermann, *Blethisa multipunctata* (Linnaeus) and *B. quadricollis* Halderman. I also studied larvae of *B. julii* LeConte recognized by association with adults (Lindroth, 1954).

Descriptive Format

The descriptive format for adults closely matches that of Whitehead (1972). Among larval instars, many characters remain unmodified (position of basic setae and pores, relative length of basic setae), but others are variously modified (microsulpture of sclerites and membrane, and number of accessory setae). The first instar larvae have peculiar characters (egg-bursters, lack of subapical and sublateral bead on the mesonotum, the metanotum and the terga 1 to 8, lack of accessory setae). Second instar larvae differ from those of the third instar in the number of accessory setae. Therefore, characters of all larvae are given under the description of "First instar larva"; those peculiar to the second instar are given under "Second instar larva"; and those of the third instar relative to those of previous instar larvae are given under "Third instar larva".

In "Taxonomic notes" I refer to number of males dissected. This number represents only the specimens for which the complete median lobe and parameres were studied. The character states of the parameres and the base of the median lobe are generally not used at specific level. However, the apex of the median lobe is an important character at the specific level, and has been examined in about 5% of males.

Descriptions of genera, subgenera and species are organized according to the postulated phylogeny starting with earliest lineages.

External Structures of Adults and Larvae

Basic external structures of adults were described by Lindroth (1969), and those of larvae by van Emden (1942). In the following discussion, unusual structures are briefly defined.

Sculpture of an elytron of *Elaphrus* consists of four rows of circular pits (depressions) and one to four rows of mirrors (strongly reflecting surfaces) (Figs. 111, 113). At the middle of each pit (except the two subhumeral pits) there is a setigerous puncture (Fig. 123). In adults of some species, the lateral edges of pits are delimited by curved ridges, in those of other species, by impressions only. Mirrors are distinctly outlined if the punctures around them are sharply separated from the mirror surface, but indistinctly outlined if the punctures are progressively more scattered toward the middle of the mirror. Mirrors are contrasted if the color of the mirror is clearly different from nearby surface color, or if nearby surface is microsculptured and dull. In this study, I retraced the origin of striae and intervals. The rows of pits and mirrors are in intervals 3, 5, 7 and 9, and areas between rows of pits are in intervals, 1, 2, 4, 6 and 8.

Setae in immatures are of two types; basic and accessory. Basic setae are found on the first instar larvae. Accessory setae on the second and third instar larvae are setae in addition to those of the first instar larvae. On larvae, pores are small circular hole-like depressions the size of a setigerous puncture. Only basic setae and pores of larvae are coded.

Except for setae on the legs, setae on adults are well understood and few in number. Thus, no special name was given to them.

In larvae, setae and pores are numerous and important in systematics. Thus, a preliminary notation system was designed. I use similar designations for apparently homologous setae and pores. This system is based on the setae and pores of first instar larvae. Those added in the second and third instars are not part of this notation system as they vary in position and number. This basic system of setae and pores, based on elaphrines, seems to be a common feature of larvae of most Carabidae. I do not follow Habu's (1961) system for head setae, as it is incomplete.

Designation of setae and pores is derived from their position. The first part of the designation denotes the position of a small group of setae and pores, and the second part, the position of the seta or pore inside the group, *i.e.*, seta PII-P of pronotum refers to a submedial group(PII) posteriorly, and to a posterior seta (-P) in the group (Fig. 76c). I did not homologize setae and pores on abdominal terga 9 and 10, and on sternum 10 with those of other abdominal segments. Codes for setae and pores are illustrated in Fig. 76a-g.

Microsculpture of adults and larvae varies considerably. Microsulpture, in this work, refers to small microscopic features about 5 to 10 microns in length. These features may be outlined by meshes (microscopic grooves). The meshed microsculpture may be roughly circular (termed isodiametric) or variously stretched (termed transverse) (Fig. 151), and its surface may be flat, subconvex, convex, scale-like, cone-like, seta-like etc. Most types of microsculpture studied are without meshes. The shapes of these features are named in relation to well known analogous objects, *i.e.,* single-pointed (tooth-like), multi-pointed (row of teeth), and others mentioned above (Figs. 152-156).

Punctures are important surface features of adults of *Elaphrus* . Punctures are circular to elongate in outline. Their diameter is expressed as the longest axis in microns (average values given in text). Their density is expressed as distance, in microns, between nearest margin of two

punctures (average values given in the text).

Most features of male genitalia have established terms. However, the enormous strut derived from the internal sac and extended through the basal orifice of the median lobe is called the stylet (Fig. 39).

I follow Noonan's (1973) terms for the ovipositor except for the two markedly sclerotized structures that form the stylus (Fig. 71). These sclerities are respectively the basal and apical sclerites. I failed to find distinguishing characters between genera in the spermatheca and its glands.

Mensural and Nominal Character States

These data were obtained for adults with a Leitz stereoscopic microscope at magnifications of 12.5, 18, 50, 72, 150 and 216 diameters using a micrometer eyepiece with a scale interval of 0.05 mm at 18 diameters.

The following abbreviations indicate the measurements made on each selected specimen:
EL –Elytral length from apex of scutellum to apex of elytron.
EW –Elytral maximum width.
PL –Pronotal length from basal margin to anterior margin along the longitudinal median stria.
PW –Pronotal maximum width.
HW –Maximum head width between the external margins of the eyes.

These measurements were used unmodified, or in ratio combinations for statistical analysis, as follow: PL/PW, PL/EL, PL/EW, PL/HW, PW/EL, PW/EW, PW/HW, EL/EW, EL/HW, EW/HW.

Atchley et al. (1976) question the use of ratios in statistical analyses, as the denominator variable of a ratio is still correlated (depending on the coefficient of variation of each variable) with the ratio. Ideally, analyses should be done with raw data by proper methods (*i.e.*, principal components and multivariate analyses), as done in some analyses with complex problems (Goulet and Baum 1981, 1982). However, ratios are easily understood by most readers, and are wisely used in infraspecific analyses as independant variables.

Measured characters were analyzed statistically. Nominal and meristic character states were expressed only as means, because the variance is much too high for interpretation (Mayr, 1969).

Descriptive Statistics

Except for one North American and one Palaearctic species each known from two specimens only, I present descriptive statistics of at least one sample of each species. For samples of eight specimens or more, I provide the following statistics of dispersion: range of variation, mean, two standard errors of the mean, 1.5 standard deviations, and coefficient of variation (Mayr, 1969). Briefly, four standard errors difference between means of two samples signify that the probability of these means being the same is only 5%, or insignificant. Thus, such difference is regarded as statistically significant. If two populations differ in a character measured by 3.0 standard deviations (assuming normal distribution), then 90% or more of the specimens in one sample are likely to be different from 90% or more of the specimens in the other sample. Such a difference is regarded as taxonomically significant at the subspecies level. When the difference observed is statistically significant, it is referred as "significant"; but when it is taxonomically distinct, it is reffered as "taxonomically significant".

I followed Whitehead (1972) in determining sample size and its assembly. Ideally, 10 males and 10 females collected in one locality at one time were used. If necessary, specimens from localities in geographically homogeneous areas were assembled to make a sample. With rare species, I used all specimens available.

Despite differences usually between means of males and females, data for each variable of both sexes are pooled. Differences in their means for linear measurements are below 5%, and those for ratios less than 1%. In this work, linear measurements are not generally significant in taxonomic analyses (see under *E. lapponicus*), but ratios are widely used in infraspecific analyses as evidence for gene flow between proximate samples. While pooling slightly increased the coefficient of variation, more was gained with larger samples in defining the mean of each variable.

Illustrations

Line drawings were made with assistance of an ocular grid in a Leitz stereoscopic dissecting microscope. For complex structures, or surface microscopic features, I used photographs taken with a Scanning Electron Microscope.

I provide maps of the distributions of all North American species, and present a brief description of ranges of Palaearctic species. Special maps were prepared to illustrate some clinal relationships and broad zoogeographic patterns.

Taxonomic Methods

Sorting of Taxa.— Adults of *Elaphrus* were first sorted according to Lindroth (1961) for North American species, to Semenov (1895), Ganglbauer (1892), Palmén (1944) and Lindroth (1939) for European species, and to Semenov (1889, 1895, 1897, 1904a, 1926) and Ohkura (1973) for Asiatic species. Then, I arranged the material of these taxa geographically for more refined intrapopulational analyses.

Criteria for Species, Subspecies.— A species is a single lineage of ancestral descendant populations of organisms which maintains its identity form other such lineages and which has its own evolutionary tendencies and historical fate (Wiley, 1978). In this study preserved specimens were used, and evidence for reproductive isolation is suggested by structural gaps between clusters of similar individuals.

Subspecies are geographically delimited populations, actually or potentially connected by gene flow. The subspecies category is reserved for populations in relatively advanced stages of speciation. In such populations, a large portion of genes will present a modified allelic distribution as well as new alleles. Such differences, if reflected phenotypically, provide the basis for subspecies recognition. This category is used when 90% or more of specimens of one population differ from those of the other.

When in doubt about populations being subspecies, vernacular names (e.g. Coastal form, Mount Rainer form) are used to simplify discussion and encourage further investigation of these geographical units.

Evidence of divergence between two geographically proximate samples is not considered proof of lack of gene flow between them. Evidence from additional neighbouring samples must also be considered. If the most geographically proximate samples of two allopatric groups of populations are most similar, or show no sign of divergence among characters studied, it was concluded that gene flow potentially or actually exists, and thus the groups are conspecific. If the most geographically proximate samples are the most divergent or are divergent in one or

more characters, it was concluded that gene flow is probably interrupted currently and two possibilities emerged. Either these samples show evidence of gene flow through neighbouring samples, in which case they are considered conspecific, or they do not, in which case they are subspecifically or specifically distinct.

Like Whitehead (1972), I found that the most meaningful statistical approach was to compare means of geographically proximate samples rather than other statistical parameters. These statistics suggest whether or not the differences between means are probably the results of coincidence.

CLASSIFICATION

TRIBE ELAPHRINI

Elaphrii Latreille, 1802:81 (*ex parte*). 1804:213. 1806:177, 227. Fairmaire and Laboulbène, 1854:6 (*ex parte*). Schaum, 1856:59 (*ex parte*).

Elaphrini Erichson, 1837:4 (*ex parte*). Schiødte, 1841:351 (*ex parte*). Letzner, 1849:50. Leconte, 1861:7. Redtenbacher, 1874:5 (*ex parte*). Dalla-Torre, 1877:22 (*ex parte*). Horn, 1881:104, 110. Bedel, 1881:21. Fauvel, 1882:23, 80. LeConte and Horn, 1883:10. Seidlitz, 1891:24, 19. Ganglbauer, 1892:121. Reitter, 1908:72, 75, 96. 1909:104. Blatchely, 1910:48. Kuhnt, 1912:49. Schaufuss, 1916:6, 29. Porta, 1923:42. Sloane, 1923:243. Portevin, 1929:40. Joy, 1932:328. La Rivers, 1946:138. Hatch, 1953:62. Lindroth, 1954:3. Ball, 1960:106. Lindroth, 1961:101. Lindroth, 1969a: XVIII, XXI. Lindroth, 1974:32.

Elaphri LeConte, 1853:401.

Elaphrides Lacordaire, 1854:41,43 (*ex parte*).

Elaphrites Jacquelin du Val, 1857:5 (*ex parte*).

Elaphrina Thomson, 1859:192. Sahlberg, 1880:10. Jacobson, 1906.266.

Elaphridae Marseul, 1880:29. Jeannel, 1941:212. Jeanne, 1966:16.

Elaphrinae Okhura, 1973:4. Freude, 1974:81.

Adults

Diagnostic combination.— Unique among adults of other tribes as in following. Metasternum with inverted V-shaped micropunctate or punctate impression medially; metepimeron present and very narrow (in some specimens fused to metepisternum); lateral ridge under elytron with apical file of longitudinal keel-like sculpture; tergum 7 with lateral pair of plates expanded apically into curved row of points; clip setae of fore-tibia curved and not sinuate.

Description.— Medium-sized to large (length of body 6.0 to 18.0 mm).

Head. Two pairs of supraorbital setae.

Mandible (Figs. 1-3) with one seta dorso-laterally in anterior third of mandibular scrobe. Outer margin of maxilla (Figs. 5–7) with three setae on basal 0.5 of stipes; palpifer with two setae on outer margin; palpomere 1, 0.4 to 0.5 as long as palpomere 2; palpomere 2, 1.5 to 1.75 as long as palpomere 3; palpomere 3, 0.5 to 1.0 as long as palpomere 4. Labium (Fig. 8) with one pair of subapical setae; paraglossae narrow, serrated on inner margin, and in most species exceeding apex of ligula; palpiger with one small ventro-basal seta; palpomere 2 with two setae. Mentum with one or two pairs of setae; medial tooth emarginate. Submentum with six or eight setae subapically.

Thorax. Pronotum with two setae on lateral margin (one pair near middle and one near hind angle), with one seta near hind angle, or setae lacking. Forecoxal cavities closed behind, and midcoxal cavities disjunct (*i.e.,* adjoining mesepimeron). Metasternum with inverted V-shaped micropunctate or punctate impression medially.

Elytron. Striae (9) of elytron completely developed, partly obsolete laterally, traceable at base, or lacking; base of stria 5 more deeply impressed basally. Basal projection of elytron with two to seven oval punctures. Setigerous punctures present on interval 9 (roughly equidistant), on scutellar stria (one puncture), on intervals 3, 3 and 5, or 3, 5 and 7. Ventral surface of elytron with longitudinal keel-like microsculpture near apex (Lindroth, 1954).

Wing. Very similar among elaphrine genera (Fig. 32).

Abdomen. Tergum 7 with fan-like plates laterally; posterior margin of plate with 11 to 25 sharp points (Gahan, 1900; Lindroth, 1954); terga 6 and 7 with a pair of basal microtrichial fields; microtrichial fields of tergum 7 extended to posterior margin. Sterna 5 and 6 with transverse basal sulcus; sterna 4, 5 and 6 with one pair of large medial setae, and sternum 7 with one or two pairs of seta on posterior margin.

Legs. Foreleg (Figs. 145 and 146). Trochanter with one, two or three setae. Tibial spurs distant, therefore, tibia of anisochaetous type and close to grade B type (for terms see Hlavac, 1971); setal band with vertical section and long (30% of tibia length, medial expansion present but not shifted far anteriorly); antennal channel shallow and developed far posteriorly to clip setae; different from grade B type in lacking confluent zone between setal band and dorsal inner fringe (ASR of Hlavac, 1971); clip setae curved but not sinuate; dorsal inner fringe dense, extended along apical 0.3 to 0.7 of tibia. First three or four tarsomeres of males slightly to moderately enlarged and with ventral spongy pubescence, or narrow and without ventral spongy pubescence.

Midleg (Figs. 147 and 148). Coxa with one, two or numerous setae. Trochanter with one, two or three setae, or setae lacking.

Hindleg. Coxa with one large seta and with one to 40 smaller setae. Trochanter with six to twelve spinules on posterior margin at base.

Male genitalia. Parameres subequal; left paramere wider than right one; ventral margin of both parameres with two rows of setae; setae extending almost to base. Opening of internal sac dorsal and subapical; interior of sac with microtrichia, brushes, fields of scales; posterior portion of sac protruding posteriorly beyond basal orifice of median lobe; protruded portion stylet-like and formed by three sclerites surrounding ejaculatory duct; ejaculatory duct inserted into stylet subapically.

Ovipositor. Stylus with basal and apical sclerites. Apical sclerite without or with one or two apical setae (Fig. 70).

All Instar Larvae

Diagnostic combination.— Recognized from larvae of other tribes as in following. Head not constricted at base, at most with shallow emargination of lateral margin between eye and base; cervical, ventro-lateral, supra-ocular and postero-ocular groove lacking; nasale pointed medially; projection of adnasale posterior to medial point of nasale; epicranial suture present. Antennae as short as mandibles. Mandible with penicillus on basal inner margin and with small seta on outer margin at level of retinaculum. Lacina conical or barely developed; seta of lacinia apical or subapical. Terga small, exposing epipleurites in dorsal view; urogomphus unarticulated, relatively slender, about as long as tergum 10. Seta of claw very short.

First Instar Larvae

Description.— Body length 4-8 mm.

Head. (Figs. 87 to 92). Egg-bursters parallel, black, keel-shaped, and extended below level of seta EM-P. Nasale pointed medially; teeth absent or very small to large. Adnasale projected moderately or slightly. Suture of frontale bisinuate. Epicranial suture 0.2 to 1.0 as long as antennal scape. Eyes with six stemmata. Antennomere 1 equal or 1.2 as long as antennomere 2, antennomere 3, 0.7 to 1.5 as long as antennomere 2, antennomere 4, 0.7 as long as antennomere 3.

Mouthparts. Mandibles sickle-shaped and with single retinaculum; penicillus on basal inner margin, and with four to seven closely associated small setae; outer margin with small seta at level of posterior margin of retinaculum. Outer margin of stipes (Fig. 83) with two large setae, one in anterior and one in posterior 0.3; inner margin of stipes with small seta posterior to lacinia; inner half of dorsal surface of stipes with 30 to 50 setae; ventral surface of stipes with one small seta near inner margin; stipes with three pores ventrally: one posterior to palpus, one centrally in basal 0.3, and one more baso-laterally. Palpomere 1 about 2.0 as long as palpifer, palpomere 2, 1.0 to 1.5 as long as palpomere 1, palpomere 3, 0.5 to 0.7 as long as palpomere 2; palpifer with small ventro-medial seta. Galea with two subequal galeomeres; galeomere 1 with ventro-subapical seta, galeomere 2 with one baso-medial and one medial microseta; seta on lacinia small or very small. Prementum (Fig. 82) dorsally with one pair of very small setae latero-subapically, and one pair of small setae medio-laterally, ventrally with one pair of very small setae baso-sublaterally. Labial palpus with two subequal palpomeres; palpomere 2 fusiform.

Thorax. Pronotum (Fig. 76c) with medial sulcus; disc darkly sclerotized; epipleuron, anterior and posterior bands thinly sclerotized; anterior band and epipleuron sharply delineated from disc, posterior band diffusely delineated; anterior and posterior bands and basal portion of epipleuron with vermiculate black pigment; anterior band with irregular longitudinal channels; lateral margin of disc without bead; disc with weakly transverse furrow, furrow ending near level of setal system ME. Prosternite strongly sclerotized, but anterior half weakly sclerotized; disc with one postero-medial pair of setae and with five to seven pairs of very small setae sublaterally. Poststernite with one seta.

Mesonotum (Fig. 76c) shorter than pronotum; medial suture present; lateral transverse sulcus absent; anterior margin beaded; epipleuron and posterior band weakly sclerotized, anterior band lacking; epipleuron sharply and posterior band diffusely delineated from disc. Mesosternite with one pair of setae. Metathorax similar to mesothorax except sculpture slightly more expanded, and anterior margin not beaded.

Membranous surfaces with pointed microsculpture over most of surface.

Abdomen. Terga 1 to 8 (Fig. 76e) with medial suture, terga 9 and 10 entire; tergum 1 widest, maximum width of each tergum tapering toward tergum 9; urogomphi as long as tergum 10, unarticulated, moderately slender, and in dorsal view

curved inward (Figs. 93a, 95 and 98a); apex of tergum 10 with two pairs of eversible sacs (one dorso-medial and one ventro-lateral pair) covered with hook-like microsculpture; terga 1 to 10 without defined anterior band or epipleuron; posterior band present on terga 1 to 9, indistinctly delineated from disc, more weakly sclerotized, with vermiculate black pigment, and without irregular longitudinal channels. Hypopleuron present on segments 1 to 8, fused to sternum on segment 9, and without setae or pores. Anterior sternite of abdomen present on segments 1 to 8, fused to sternum 9, and with one very small seta. Sternite and posternites separated on segments 1 to 7, and fused together on segments 8 to 10; sternite on segments 1 to 8 with one pair of setae, sternite 9 without setae. Inner poststernite with two setae. Outer poststernite with two setae except on segment 1 with anterior seta only.

Legs. Tarsus with one pair of subequal claws; claw with one very small seta.

Second Instar Larvae

Description.— Linear measurements about 1.5 times as long as those of first instar larvae of same species. Numerous accessory setae present over most sclerites in addition to basic setae and pores.

Head. Ventral surface of parietale with two fields of isodiametric or slightly transverse sculpture, one medial and one lateral to systems VMM and VMP. Egg-bursters lacking.

Thorax. Anterior band of pronotum and prosternum with irregular longitudinal channels on disc. Posterior margin of prosternum beaded. Subapex of mesonotum with transverse bead extended antero-sublaterally. Anterior sternite of mesothorax with one to three accessory setae. Metathorax as above but pointed sculpture slightly more expanded and accessory setae slightly more numerous in most species. Pointed micro-sculpture widespread on membranous surfaces.

Abdomen. Terga 1 to 8 with transverse bead extended sub-basally and sublaterally; posterior band with or without irregular longitudinal channels; urogomphus with 14 to 50 setigerous punctures.

Third Instar Larvae

Description.— Linear measurements about 1.5 times longer than those of second instar larvae of same species. Accessory setae of most sclerites more numerous than those of second instar larvae of same species.

Geographical Distribution and Affinities, and Notes

Distribution.— Species of this tribe live in all regions of the northern hemisphere (except for Greenland and Iceland) from the southern edge of the tundra to the southern half of the temperate zone (southern California, northernmost Florida, Morocco). Few species occur in subhumid regions and none are found in desert regions.

NOTES ABOUT KEYS

Larvae are best studied in glycerin. They may also be studied in alcohol, though many characters are not readily seen. Setae are divided into four size classes: very small, small, medium-sized and large. Examples of these size classes are shown on the maxilla (Fig. 83b). I provide five keys: one to genera, one to subgenera of *Elaphrus* and three to species of these subgenera. Lindroth (1954) provided means of identification for known adults and larvae of species of *Diacheila* and *Blethisa.*

Key to genera of Elaphrini

Adults

1 Lateral margin of pronotum with two pairs of setae (one near middle and one near hind angle). Elytral striae well developed on disc (Figs. 28, 29 and 30); setigerous punctures present on elytral intervals 3,5 and 9 or 3 and 9. Middle coxa with one or two setae. Eyes small or moderate; medial margins lower than frons 2

1′ Lateral margin of pronotum with one pair of setae near hind angle or setae

lacking. Elytral striae barely suggested near base or absent (Figs. 110 to 117); setigerous punctures present on elytral intervals 3, 5, 7 and 9. Middle coxa with numerous setae. Eyes large; medial margins higher than frons ..... *Elaphrus* Fabricius p. 238

2 (1) Lateral portion of pronotum not explanate. Elytral interval 3 not catenate (Fig. 28); setigerous punctures present on elytral intervals 3 and 9. Fronto-ocular sulcus very shallowly impressed and linear (Fig. 14). Clypeus without impression. Mentum with one pair of setae (Fig. 8) ..... *Diacheila* Motschulsky p. 235

2′ Lateral portion of pronotum explanate. Elytral intervals 3 and 5 catenate (Figs. 29 and 30); setigerous punctures present on elytral intervals 3, 5 and 9. Fronto-ocular sulcus sharply impressed and eight-shaped (Fig. 15). Clypeus with sublateral impressions. Mentum with 2 pairs of setae (Fig. 9) ..... *Blethisa* Bonelli p. 236

All Instar Larvae

1 Lacinia well developed and cone-shaped (Figs. 83c and 84). Base of mandible narrow: basal inner margin apparently continuous with apical inner margin (Fig. 78) 2

1′ Lacinia suggested or absent (Figs. 85c and 86). Base of mandible wide: basal inner margin not in line with apical inner margin (Figs. 80 and 81) ..... *Elaphrus* Fabricius p. 238

2 (1) Teeth of nasale small (Fig. 87a). Ventral surface of stipes with membranous declivity laterally behind postero-lateral seta ..... *Diacheila* Motschulsky p. 235

2′ Teeth of nasale large (Fig. 88b). Ventral surface of stipes completely sclerotized ..... *Blethisa* Bonelli p. 236

DISTINCTION OF SEX IN ADULTS

Adult males, except in those of *E. punctatus* which lack any secondary sexual characters, are recognized by enlarged basal tarsomeres of forelegs with white hair-like structures ventrally, termed spongy pubescence. In most species, males have a small tooth-like projection at the base of inner spur of the midtibia; in some species, males are more densely setose centrally on abdominal sterna than females; in a few species, males have tooth-like projections at base of apical spur and of posterior spur of foretibia, or only at base of posterior spur; in one species, males have a large ventral projection on forefemur.

DISTINCTION OF LARVAL INSTARS

Recognition of first larval instar is easy, but separation of the second from third instar larvae is difficult. Except for a greater number of accessory setae on most sclerites in the third instar than the second instar larvae of each species, no other differences were found. However, the number of accessory setae is different between species of the same instar. Therefore, the segregation of these instars of Elaphrini is possible only after determination of the genus and

subgenus. Fortunately, genera and subgenera are recognized by characters common to all instar larvae (see keys of genera of Elaphrini and subgenera of *Elaphrus* respectively on p. 233 and p. 240). The following key provides necessary information for segregating all instars of known species of elaphrine larvae. In couplet 2 locate the genus or subgenus of the specimen, then compare couplet 2 and 2′ for this genus or subgenus. Characters in couplet 2 describe second instar larvae, and those in couplet 2′, third instar larvae. Male and female larvae are not distinguishable by external structures.

Key for recognition of larval instars

1 Egg-bursters present as parallel black carinae sublaterally on frontale (Fig. 87). Mesonotum, metanotum and terga 1 to 8 without transverse submarginal bead along anterior and lateral margins (Figs. 76c, 76e). Only basic setae and pores present on sclerites as illustrated (Fig. 76). Urogomphus with five large and one very small setae ..... First instar

1′ Egg-bursters absent from frontale. Mesonotum, metanotum and terga 1 to 8 with transverse submarginal bead along anterior and lateral margins. Many accessory setae present on most sclerites in addition to basic setae and pores of first instar. Urogomphus with seven to 30 major accessory setae (Figs. 93b, 94, 96, 98b, 99, 100, 101 and 103). Second or third instar 2

2 (1′) *Diacheila.* - Projections on urogomphus half as large as those of third instar larvae (Fig. 93b).

Blethisa. - Pronotal epipleuron with 20 accessory setae or less, on mesonotal epipleuron with 15 or less, sternite of segments 2 to 7 with 40 or less, and outer poststernite of segments 2 to 7 with 10 or less.

Elaphrus (Arctelaphrus). - Head width 0.8 mm. (I have not seen the second instar larva, but number of accessory setae probably follows a pattern similar to members of subgenus *Elaphrus* , thus I assume the following would apply). Each sclerite of mesonotum and metanotum with 10 accessory setae or less, epipleuron of abdominal segments 2 to 8 with 10 or less, sternite of segment 9 without, and outer poststernite of segments 2 to 7 with five or less.

Elaphrus (Neoelaphrus). - Proepisternum with five accessory setae or less, each sclerite of mesonotum and metanotum with 15 or less, and outer poststernite of segments 2 to 7 with seven or less.

Elaphrus (Elaphrus). - Each sclerite of pronotum with 15 accessory setae or less, each sclerite of mesonotum and metanotum with 10 or less, each sclerite of terga 1 to 8 with nine or less, hypopleuron of abdominal segments 2 to 8 with four or less, and sternite of abdominal segments 2 to 8 with ten or less. Urogomphus with largest projection half as large as that on third instar larvae (Fig. 100).

Elaphrus (Elaphroterus). - Proepisternum with seven accessory setae or less, each sclerite of terga 1 to 8 with 30 or less, hypopleuron of abdominal segments 2 to 8 with eight or less, sternite of abdominal segments 2 to 8 with 14 or less, and outer poststernite of segments 2 to 7 with four or less

Second instar

2′ *Diacheila*. - Largest projection of urogomphus large (Fig. 94).

Blethisa. - Pronotal epipleuron with 30 accessory setae or more, each sclerite of mesonotum with 90 or more, mesonotal epipleuron with 20 or more, sternite of abdominal segments 2 to 7 with 90 or more, and outer poststernite of segments 1 to 7 with 30 or more.

Elaphrus (Arctelaphrus). - Head width 1.1 mm. Each sclerite of mesonotum and metanotum with 16 accessory setae, epipleuron of abdominal segments 2 to 8 with 18, sternite of abdominal segment 9 with eight, and outer poststernite on segments 2 to 7 with seven.

Elaphrus (Neoelaphrus). - Proepisternum with 25 accessory setae or more, each sclerite of mesonotum and metanotum with 25 or more, and outer poststernite of segments 2 to 7 with nine or more.

Elaphrus (Elaphrus). - Each sclerite of pronotum, mesonotum and metanotum with 21 accessory setae or more, each sclerite of terga 1 to 8 with 17 or more, hypopleuron of abdominal segments 2 to 8 with eight or more, and sternites of abdominal segments 2 to 8 with 14 or more. Largest projection of urogomphus large (Fig. 100).

Elaphrus (Elaphroterus). - Proepisternum with 10 accessory setae or more, each sclerite of terga 1 to 8 with 40 or more, hypopleuron of abdominal segments 2 to 8 with 12 more, sternite of abdominal segments 2 to 8 with 28 or more, and outer poststernite of segments 2 to 7 with seven or more .

. . . . . Third instar

Genus *Diacheila* Motschulsky

Figs. 2, 5, 8, 14, 28, 38, 70, 78, 79, 83a-c, 84, 87a-b, 93a-b, 94

Diacheila Motschulsky, 1846:12. Type-species: *Harpalus arcticus* Gyllenhal, 1810, fixed by Lindroth (1961), by subsequent designation. Lindroth, 1961:102.

Diaheila Motschulsky, 1846:74. Lindroth, 1961:102 (invalid emendation).

Diachila; Motschulsky, 1846. Schaupp, 1878:29. Marseul, 1880:67. Horn, 1881:111 Marseul. 1882:4. LeConte and Horn, 1883:11. Jacobson, 1906:267. Lindroth, 1954:3, 4. Ball, 1960:106 (invalid emendation).

Arctobia Thomson, 1859:3, 194. Type-species: *Harpalus arcticus* Gyllenhal, 1810, fixed by Thomson (1859), by monotypy. Marseul, 1882:4. Lindroth, 1954:4.

Adults

Diagnostic combination.— Distinguished from other elaphrine beetles by presence of setigerous punctures on intervals 3 and 9 only, and by dissociated striae 2 and 3 of elytron.

Description.— Medium-sized 7.0 to 9.0 mm.

Head. Eye moderate or small, medial margin lower than frons. Fronto-ocular sulcus very shallowly impressed (Fig. 14). Clypeus without impression.Apical retinacular and basal terebral tooth of right mandible small (Fig. 2). Maxillary palpomere 3, 0.5 as long as palpomere 4 (Fig. 5). Mentum (Fig. 8) with one pair of setae.

Thorax. Pronotum with lateral portion not explanate and with two pairs of setae; lateral bead narrow or wide. Scutellum without transverse ridge basally. Mesosternum without postero-lateral ridge. Posterolateral setae of metanotum very small.

Abdomen. Tergum 2 with one pair of postero-submedial ridge. Tergum 1 without setae. Abdominal sternum 7 with one pair of setae on posterior margin.

Elytron. Most striae clearly defined on disc; striae 2 and 3 dissociated from base to subapex (Fig. 28); interval 3 not catenate. Surface of intervals smooth near setigerous punctures and equally brilliant. Setigerous punctures small (20 microns), round, without antero-medial cuticular prominence, restricted to intervals 3 and 9; interval 3 and 9 respectively with four to seven and with six to ten setigerous punctures. Punctures restricted to striae.

Wing. Similar to that of species of *Blethisa* with rounded posterior end of oblongum (see Fig. 33).

Legs. Foreleg: trochanter with two setae, femur with 20 setae or less, fringe on medio-dorsal surface of tibial in apical 0.4 to 0.5. Midleg: coxa with two setae, trochanter with one seta, femur with 20 setae or less. Hindleg: coxa with three setae.

Male genitalia. Median lobe (Fig. 38) markedly sclerotized generally and becoming weakly sclerotized dorso-apically. Stylet of internal sac narrow, short, and not spatulate anteriorly.

Ovipositor. Basal sclerite of stylus with defined lateral and medial ridges dorsally, and with small setae on dorsal ridges and apico-ventral surface. Apical sclerite with few small setae, apex with two small setae (Fig. 70).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other elaphrine genera by well developed and conical lacinia (Figs. 83c and 84), and small teeth on nasale (Fig. 87b).

Description.— Ultimate length 7 to 10 mm. Medial portion of nasale slightly or moderately projected; teeth on nasale fine; base of mandible narrow, and basal inner margin seemingly continuous with apical inner margin. Lacinia well developed and conical; seta apical and small, or subapical and very small. Ventral surface of stipes with membranous declivity behind postero-lateral seta (Fig. 83b).

Geographical Distribution and Affinities, and Notes

Distribution.— Species of this Holarctic genus live in subarctic and southern arctic regions, from Scandinavia through Siberia, and from Alaska to Labrador. One relict species occurs along the Tien-Shan mountains in Western China and neighbouring USSR (Lindroth, 1954).

Taxonomic notes.— Lindroth (1954) recognized three extant species. I studied in detail adults of two of them: *Diacheila arctica* Gyllenhal and *D. polita* Faldermann, and briefly those of *D. fausti* Heyden . I will not discuss the species further as Lindroth's review is most satisfactory. Lindroth (1954) described the larva of *D. arctica* and Sharova (1958) described that of *D. polita* (confirmed by my own rearing). I examined six first instar and three second instar larvae of *D. polita* from the Anderson River delta, NWT. I failed to locate the larva of *D. arctica* studied by Lindroth. Since the data on *D. arctica* were insufficient, I was unable to characterize more fully larvae of the genus; thus the description is only partially comparable with that of other genera.

Genus *Blethisa* Bonelli

Figs. 1a-b, 6, 9, 15, 29, 30, 33, 39a-d, 71, 88a-b, 95, 96a-b

Blethisa Bonelli, 1810. Type-species: *Carabus multipunctatus* Linnaeus, 1758, fixed by Bonelli (1810), by monotypy. Dejean, 1826:3, 265. Dejean and Boisduval, 1830:119. Heer, 1838:39 *(ex parte)*. Motschulsky, 1846:74. LeConte, 1850:208. 1853:401. Lacordaire, 1854:44 *(ex parte)*. Schaum, 1856:75. Jacquelin du Val, 1857:6 *(ex parte)*. Thomson, 1859:3, 194. LeConte, 1861:7. Crotch, 1873:4. Redtenbacher, 1874:6. Seidlitz, 1875:3. Dalla-Torre, 1877:23. Schaupp, 1878:29. Marseul, 1880:33 *(ex parte)*. Horn, 1881:111. Bedel, 1881:21, 22. Fauvel, 1882:81, 85. Marseul, 1882:4. LeConte, 1883:11. Seidlitz, 1891:4, 19. Ganglbauer, 1892:121. Everts, 1898:48. Jacobson, 1906:266. Reitter, 1908:96,97. 1909:106. Blatchley, 1910:49. Kuhnt, 1912:31, 49. Fairmaire, 1913:30. Schaufuss, 1916:28,29. Porta, 1923:78. Portevin, 1929:41. Jacobson, 1931:82. Joy, 1932:328. Jeannel, 1941:215. Lindroth, 1954:3, 10. Ball, 1960:106. Lindroth, 1961:104. Ohkura, 1973:4. Lindroth, 1974:32.

Helobium Leach, 1815:83. Type-species: *Carabus multipunctatus* Linnaeus, 1758, fixed by Leach (1815), by monotypy. Lindroth, 1961: 104. Lindroth, 1974:32.

Rhaphiona Fisher von Waldheim, 1829:34. Type-species: *Blethisa eschscholtzi* Zoubkoff, 1829, fixed by Fisher von Waldheim (1829), by monotypy. Lindroth, 1961:104.

Adults

Diagnostic combination.— Distinguished from other elaphrine beetles by deeply impressed fronto-ocular sulcus (shaped as a fiqure 8, see Fig. 15), by weakly impressed clypeus sublaterally, by long maxillary palpomere 3 (0.7 as long as palpomere 4), by two pairs of setae

on mentum, by explanate lateral portion of pronotum, by presence of setigerous punctures on elytral intervals 3, 5 and 9, and by one seta on femur of hind leg.

Description.— Medium to large beetles: 10 to 18 mm.

Head. Eye well developed, medial margin lower than frons. Fronto-ocular sulcus deeply impressed and shaped as a figure 8 (Fig. 15). Clypeus with weak sublateral impressions. Apical retinacular and basal terebral tooth of right mandible small or large, (Fig. 1). Maxillary palpomere 3, 0.7 length of palpomere 4 (Fig. 6). Mentum (Fig. 9) with 2 pairs of setae.

Thorax. Pronotum with lateral portion explanate and with two pairs of setae. Scutellum with transverse ridge basally. Postero-lateral ridge of mesosternum well developed. Postero-lateral setae of metanotum medium-sized.

Abdomen. Tergum 2 without postero-medial ridge. Tergum 1 with numerous setae. Abdominal sternum 7 with two pairs of setae on posterior margin.

Elytron. Striae 1-6 well defined, remaining striae slightly expressed, irregularly interrupted, or obsolete; intervals 3 and 5 catenate (Figs. 28, 29). Surface between two setigerous punctures brighter than that of proximate intervals (mirror-like), or not brighter; surface near setigerous puncture flat or elevated, but not pit-like. Setigerous punctures large (50 to 60 microns in diameter), antero-medially emarginated and elevated, restricted to elytral intervals 3, 5 and 9; interval 3 with five or six, interval 5 with two to four, and interval 9 with nine to nineteen setigerous punctures; setigerous punctures small. Punctures restricted to striae.

Wing. Similar to that of species of *Diacheila* with rounded posterior end of oblongum (Fig. 33).

Legs. Foreleg: trochanter with one seta, femur with 16 setae or less, fringe on medio-dorsal surface of tibia on apical 0.3. Midleg: coxa with one or two setae, trochanter with one or without setae, femur with 20 setae or less. Hing leg: coxa with two setae.

Male genitalia. Baso-lateral and ventral surface of median lobe markedly sclerotized, and sharply delimited from weakly sclerotized dorsal surface (Fig. 39). Stylet of internal sac large, protruded well beyond basal orifice, and spatulate anteriorly.

Ovipositor. Basal sclerite of stylus without lateral and medial ridges dorsally, and with numerous setae in apical 0.7 (Fig. 71). Apical sclerite with many very small spinules on surface, apex with two small setae.

All Instar Larvae

Diagnostic combination.— Distinguished from the larvae of other elaphrine genera by large and conical lacina, and large teeth on nasale (Fig. 88b).

First Instar Larvae

Description.— Ultimate length 7 to 10 mm. Medial portion of nasale obtusely pointed (Fig. 88a), teeth of nasale large and occupying all of anterior margin. Angle formed by seta DI-A and pores DI-P and DMP-E about 160°. Base of mandible narrow, and basal inner margin seemingly continuous with apical inner margin. Lacinia large and conical; seta subapical and very small. Ventral surface of stipes completely sclerotized. Microsculpture of urogomphus scale-like.

Second and Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of other genera by divided epipleuron on abdominal segments 1 to 8, and presence of accessory setae on the ventral surface of stipes.

Second Instar Larvae

Description.— Ultimate length 9 to 15 mm. Accessory setae present on ventral surface of stipes. Each sclerite of pronotum and mesonotum respectively with about 95 and with 60 to 70 accessory setae. Abdominal epipleuron of segments 1 to 8 divided in two.

Third Instar Larvae

Description.— Ultimate length 15 to 23 mm. Each sclerite of mesonotum with 90 to 110 accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— Species of this Holarctic genus are found in arctic, boreal and temperate regions, from the British Isles to Kamchatka, and from Alaska to Newfoundland (Lindroth, 1954).

Taxonomic notes.— Adults of species of this genus were revised by Lindroth (1954). Goulet and Smetana (1983) characterized one additional species and proposed a phylogeny and zoogeography for species of the genus.

Larvae of *B. multipunctata* and *B. julii* are similar. Characters presented in Lindroth's (1954) key are difficult to interpret or are variable. The larvae of these species are characterized as in the following. In larvae of *B. julii,* the apical teeth of nasale are fused into one large tooth (Lindroth, 1954:21, Fig. 11b) and the miscrosculpture is less developed on mesonotum and metanotum (pointed sculpture near suture is barely developed in second instar larvae, absent in third instar larvae, and suggested or absent antero-laterally). In larvae of *B. multipunctata,* the apical teeth of nasale are separated by a very small sharp tooth medially (Lindroth, 1954:21; Fig. 11c) and the microsculpture is more widespread on mesonotum and metanotum (pointed sculpture along suture forms a wide band in second instar larvae or a narrow band in third instar larvae, and is widely developed antero-laterally). This augments Lindroth's key (1954:23, 24).

I have seen adults of all species of *Blethisa* reviewed by Lindroth (1954). I examined four first instar, three second instar, and three third instar larvae of *B. quadricollis* Haldeman from the junction of the Athabasca River with Highway 2, Alberta; six first instar, two second instar, and three third instar larvae of *B. multipunctata* Linnaeus from George Lake, Alberta; five second instar larvae of *B. julii* LeConte from three localities in Newfoundland, and two third instar larvae of *B. julii* from two localities in Newfoundland.

Genus *Elaphrus* Fabricius

Elaphrus Fabricius, 1775:227. Type-species: *Cicindela riparia* Linnaeus, , 1758, fixed by Latreille (1810), by subsequent designation. Rossi, 1790:193. Olivier, 1790:4 *(ex parte).* Latreille, 1796:75 *(ex parte).* Illiger, 1798:225 *(ex parte).* Fabricius, 1801:245 *(ex parte).* Latreille, 1802:81 *(ex parte).* 1804:214. 1810:158 *(ex parte).* Gyllenhal, 1810:6 *(ex parte).* Dejean, 1826:3, 268. Curtis, 1827:19. Erichson, 1837:3. Dejean and Boisduval, 1830:124. Heer, 1838:39 *(ex parte).* Schiødte, 1841:356. Küster, 1846:7; Letzner, 1849:50. LeConte, 1850:209. 1853:401, 402. Fairmaire and Laboulbène, 1854:6. Lacordaire, 1854:44 *(ex parte).* Schaum, 1856:68. Jacquelin du Val, 1857:6. Thomson, 1859:3, 192. LeConte, 1861:7. Stierlin, 1869:10. Crotch, 1873:4. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Schaupp, 1878:6. Marseul, 1880:29. Horn, 1881:111. Bedel, 1881:22. Fauvel, 1882:81. LeConte and Horn, 1883:10. Marseul, 1882:4. Seidlitz, 1891:4, 19. Ganglbauer, 1892:122. Semenov, 1895:305. Everts, 1898:48. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:104. Blatchley, 1910:48. Kuhnt, 1912:31, 50. Fairmaire, 1913:30. Schaufuss, 1916:28, 29. Porta, 1923:78. Semenov, 1926:39. Portevin, 1929:40. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:216. Hatch, 1953:63. Lindroth, 1954:3. Antoine, 1955:47. Ball, 1960:108. Nakane *et al.*, 1963:19. Ohkura, 1973:4. Lindroth, 1974:32.

Adults

Diagnostic combination.— Distinguished from other elaphrines by large eyes, by lack of striae on elytra (in some species suggested at base), and by presence of setigerous punctures on intervals 3, 5, 7 and 9.

Description.— Medium-sized: 6 to 10 mm.

Head. Eye large, medial margin of eye higher than frons. Fronto-ocular sulcus indistinct (Fig. 16). Clypeus without impression. Apical retinacular tooth of right mandible single or double, and its basal terebral tooth prominent (Figs. 3 and 4). Maxillary palpomere 3, 0.3 to 0.5 as long as palpomere 4 (Fig. 7). Mentum (Fig. 10) with one pair of setae.

Thorax. Pronotum with lateral margin not explanate, and with one seta or without seta. Scutellum without transverse ridge basally. Postero-lateral ridge of mesosternum weakly developed or absent. Postero-lateral setae of metanotum small to very small.

Abdomen. Tergum 2 with one pair of submedial ridges posteriorly. Tergum 1 without setae. Abdominal sternum 7 with one or two pairs of setae on posterior margin.

Elytron. Striae barely traceable at base or absent. (Figs. 31, 110 to 117); intervals not clearly delineated, but intervals 3, 5, 7 and 9 outlined by alternation of crater-like impressions (pits) and brilliant surface (mirror). Pits delimited externally by punctures in semicircular stria, by depressions between intervals, by contrasting color (golden-copper band), or by elongate punctures; base of elytron with two pits lacking setigerous punctures on intervals 5 and 7; scutellar setigerous punctures elevated, but not situated in circular pit. Mirrors (when present) situated between two pits of same interval; each elytron with one to 20 mirrors. Surface with four rows of pits bearing central setigerous puncture in intervals 3, 5, 7 and 9; interval 3 with five or six setigerous punctures, interval 5 with four, interval 7 with four, and interval 9 with seven or eight. Setigerous punctures large (40 to 50 microns, smaller in *E. lapponicus*) , antero-medially emarginate and elevated. Punctures present over elytra except on mirrors.

Wings. Venation similar to that of species of other genera except for subangular posterior end of oblongum (Fig. 32).

Legs. Foreleg: trochanter with one, two or three setae, femur (Figs. 145 and 146) with 30 setae or more, fringe on medio-dorsal surface of tibia on apical 0.5 to 0.8. Midleg: coxa with numerous setae, trochanter with one, two or three setae, femur (Figs. 147 and 148) with 27 setae or more. Hindleg: coxa with three to 40 setae.

Male genitalia. Baso-lateral and ventral surface of median lobe strongly sclerotized, and sharply delineated from weakly sclerotized dorsal surface (Fig. 40a). Stylet of internal sac large, protruded well beyond basal orifice, and spatulate anteriorly.

Ovipositor. Basal sclerite of stylus with lateral and medial ridges dorsally, with small setae on dorsal ridges, and with or without setae apically. Apical sclerite of stylus with two to six very small stout setae along dorsal ridges, apex without or with one or two very small setae (Figs. 72 to 75).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other elaphrine genera by barely suggested lacinia, and by enlarged basal inner margin of mandible (therefore, basal margin not directly in line with apical one).

First Instar Larvae

Description.— Ultimate length 6 to 7 mm. Medial portion of nasale subacutely or acutely pointed, teeth absent or present; teeth very fine, fine or medium-sized, and lacking medially (Figs. 89b to 92b). Angle formed by setae DI-A, and pores DI-P and DMP-E 130°or less. Base of mandible enlarged, and basal inner margin not in line with apical inner margin (Figs. 80 and 81). Lacinia barely suggested (Fig. 85c); seta apical and small. Ventral surface of stipes with membranous declivity behind postero-lateral seta, or completely sclerotized. Microsculpture of urogomphus single-pointed or lacking.

Second Instar Larvae

Description.— Ultimate length 7 to 9 mm. Accessory setae absent from ventral surface of stipes. Each sclerite of pronotum and mesonotum respectively with 15 to 45 and with 8 to 40 accessory setae. Abdominal epipleuron of segments 1 to 8 entire.

Third Instar Larvae

Description.— Ultimate length 11 to 15 mm. Each sclerite of mesonotum with 25 to 100 assessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— Species of this Holarctic genus live in arctic, boreal and temperate regions, from the British Isles to Kamchatka, and from Alaska to Newfoundland.

Key to subgenera of *Elaphrus* Fabricius

Adults

1 Fringe of setae on posterior margin of pronotum extended to posterior angle (Figs. 20 to 25). Suture between proepisternum and proepimeron not evident. Males with first three tarsomeres slightly expanded and with

spongy pubescence ventrally, or not expanded and without spongy pubescence 2

1′ Fringe of setae on posterior margin of pronotum not reaching posterior angle (Figs. 17 to 19). Suture between proepisternum and proepimeron evident. Males with first four tarsomeres slightly expanded and with spongy pubescence ventrally 3

2 (1) Clypeus with four to six setigerous punctures. Disc of prosternum and process of mesosternum with setae. Trochanter of foreleg and midleg with three setigerous punctures. Coxa of hindleg with setae covering surface .. .. *Elaphrus* Fabricius p. 282

2′ Clypeus with two setigerous punctures. Disc of prosternum and process of mesosternum asetose. Trochanter of foreleg with two, that of midleg with one or two setigerous punctures. Coxa of hindleg with setae restricted to mesial half of surface. ..... *Elaphroterus* Semenov p. 322

3 (1′) Maxillary palpomere 3, 0.5 as long as palpomere 4. Disc of prosternum and lateral portion of metasternum setose. Elytral pits with one to six irregularly arranged punctures (Fig. 131). Microsculpture on elytra strongly convex and widespread ..... *Arctelaphrus* Semenov p. 241

3′ Maxillary palpomere 3, 0.3 as long as palpomere 4. Disc of prosternum and lateral portion of metasternum asetose. Elytral pits with at least eight regularly distributed punctures (Figs. 132 to 136). Microsculpture on elytra at most convex and not covering entire surface .... *Neoelaphrus* Hatch p. 246

All instar larvae

1 Head elongate: bisinuation of lateral margin behind eye with anterior convexity longer than posterior one (Figs. 89a and 90a). Epicranial suture at least 0.7 as long as antennal scape. Medial point of nasale obtused (Figs. 89b to 90b). Maxillary palpomere 1, 1.5 (first and second instar larvae) or 1.2 (third instar larvae) as long as palpomere 2. Baso-ventral pores of stipes distant: submedial pore situated distinctly anterior to sublateral one (Fig. 85b) 2

1′ Head short: bisinuation of lateral margin behind eye with anterior and posterior convexities subequal (Figs. 91a and 92a). Epicranial suture no more than 0.6 as long as antennal scape. Medial point of nasale acute (91b and 92b). Maxillary palpomere 1, 1.0 (first instar larva), or 0.8 (second instar larva), or 0.7 (third instar larva) as long as palpomere 2. Baso-ventral pores of stipes adjacent: submedial pore slightly anterior to external one (Fig. 83b) 3

2 (1) Ventral surface of stipes with membranous embayment behind posterolateral seta (Fig. 83b). Mesonotal and metanotal seta PII-P very small; anterior seta of outer poststernite of segment 9 very small .... *Arctelaphrus* Semenov p. 241

2′ Ventral surface of stipes entirely sclerotized (Fig. 85b). Mesonotal and metanotal seta PII-P small; anterior seta of outer poststernite of segment 9

medium-sized ..... *Neoelaphrus* Hatch p. 246

3 (1′) Teeth of nasale absent or fine (Fig. 91b). Posterior band of mesonotum and metanotum with pointed sculpture on 0.3 of its surface. Inner seta of inner poststernite on segments 1 to 9 very small .... *Elaphrus* Fabricius p. 282

4′ Teeth of nasale present and slightly coarser than in larvae of subgenus *Elaphrus* (Fig. 92b). Posterior band of mesonotum and metanotum with pointed sculpture on 0.5 or more of its surface. Inner seta of inner poststernite on segment 1 to 8 small, that on segment 9 clearly larger .... *Elaphroterus* Semenov p. 322

Subgenus *Arctelaphrus* Semenov

Arctelaphrus Semenov, 1926:39. Type-species: *Elaphrus lapponicus* Gyllenhal, 1810, fixed by Semenov (1926), by original designation. Ball, 1960:106. Lindroth, 1961:111.
Elaphrus Semenov, 1895:309. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:104. Bänninger, 1919:149. *Ex Parte.*

Adults

Diagnostic combination.— Distinguished from adults of other subgenera as in following. Disc of prosternum setose. Suture between proepisternum and proepimeron sharply delineated. Setigerous punctures in intervals 3, 5 and 7 small (25 microns in diameter), others large (40 to 50 microns in diameter). Elytral pits (Fig. 31) with a few irregularly arranged punctures.

Description.— *Head.* Frons without medial fovea. Clypeus with one pair of setae. Terebral margin of right mandible 0.3 as long as mandible (Fig. 3); basal retinacular tooth emarginate; apex of retinacular tooth situated anteriad of terebral tooth. Maxillary palpomere 3, 0.5 as long as palpomere 4. Galeomere 1 subequal to maxillary palpomere 2.

Thorax. Lateral margin of pronotum completely beaded. Fringe of setae on posterior margin not extended to hind angles; setae of fringe scimitar-shaped and narrow. Suture between proepisternum and proepimeron sharply delineated. Disc and apophysis of prosternum setose. Process of mesosternum asetose; postero-lateral ridge of mesosternum outlined.

Abdomen. Tergum 7 without setae.

Elytron. Striae indistinct at base (Fig. 110). Transverse basal stria sharply outlined at shoulder. Setigerous punctures of intervals 3, 5 and 7, 25 microns in diameter, those of interval 9 and scutellar interval 40 to 50 microns in diameter. Mirrors of interval 3 subequal in width. Elytral pits with few irregularly arranged punctures (Fig. 131).

Legs. Foreleg: trochanter with two setae; femur with about 70 setae; tibia with about 34 setae; inner dorsal fringe of tibia 0.5 as long as tibia, and with about eight setae posteriorly; first four tarsomeres of males with spongy pubescence ventrally. Midleg: coxa with few accessory setae; trochanter with one or two setae; femur with about 75 setae; tibia with about 80 setae. Hindleg: coxa with about 10 setae on inner 0.5 of process; femur with about 20 setae; tibia with about 125 setae.

Male genitalia. Internal sac of median lobe with large scales posteriorly.

Ovipositor. Basal sclerite of stylus with some very small setae ventrally; apical sclerite with few stout setae on dorso-lateral and dorso-medial ridges, and apex with two very small setae (Fig. 72).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other subgenera as in following. Epicranial suture as long as or longer than antennal scape (Fig. 89a). Ventral surface of stipes with membranous declivity behind posterior seta, and with two posterior pores distant (Fig. 85b).

First Instar Larvae

Description.— Medial point of nasale obtuse; teeth of nasale large and terminated subapically on medial point (Fig. 89b). Epicranial suture subequal to or longer than antennal scape (Fig.89a). Head elongate: bisinuation behind eye with anterior convexity longer than posterior one. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 110° to 130°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale equilateral. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin asetose; dorsal surface with about 30 setae on inner 0.5, subapical setae roughly distributed in one row; two postero-ventral pores distant (Fig. 85b).

Second Instar Larvae

Not seen, but briefly described by Luff (1976); similar to third instar larvae except for smaller head (width 0.8 mm). I assume this instar can be recognized, as in nearly all species of *Elaphrus,* by smaller projections on urogomphus (largest one about 0.5 size of that of third instar).

Third Instar Larvae

Description.— Prementum with less than two setae dorso-laterally. Proepisternum with 15 accessory setae. Largest projection of urogomphus in lateral view medium-size (Fig. 97). Each sclerite of terga 1 to 8 with about 37 accessory setae. Hypopleuron of abdominal segments 1 to 8 each with 19 accessory setae. Sternite of abdominal segment 1 with two accessory setae, those of segments 2 to 7 each with about 22, those of segments 8, 9 and 10 respectively with 30, nine and eight.

Geographical Distribution and Affinities, and Notes

Distribution.— The Holarctic range of the only species of this subgenus is restricted to subarctic regions.

Elaphrus lapponicus Gyllenhal

Diagnostic combination.— Setigerous punctures on intervals 3, 5 and 7 small (25 microns in diameter). Elytron with very convex microsculpture; pits clearly outlined by punctures, each with few irregular punctures (Figs. 118 and 131).

Elaphrus lapponicus lapponicus Gyllenhal new status
Figs. 3a-b, 7, 10, 16, 31, 72, 89a-b, 97, 110,157

Elaphrus lapponicus Gyllenhal, 1810:8. Type locality: Lappland, subsequently restricted to Abisko, Sweden, (Lindroth 1961); type in Göteborg Museum; seen by Lindroth (1961). Dejean, 1826:73. Gyllenhal, 1827:397. Schaum, 1856:70. Seidlitz, 1875:2. Marseul, 1882:4. Semenov, 1895:310. Jacobson, 1906:267. Joy, 1932:328. Lindroth, 1961:111. 1974:32.

Elaphrus elongatus Fischer von Waldheim, 1828:266. Type locality: Kamchatka, USSR; type in Zoological Museum, University, Helsinki; seen by Lindroth (1961). Marseul, 1882:4. Lindroth, 1961:111.

Elaphrus elongatus; Semenov, 1895:310.

Elaphrus obscurior Kirby, 1837:63. Type locality: Latitude 65°– according to Lindroth (1961) near Great Bear Lake, N.W.T.; type in British Museum of Natural History, London; type seen by Lindroth (1961). Crotch, 1876:246. Schaupp, 1878:6. Marseul, 1882:4. Lindroth, 1961.111.

Elaphrus lapponicus var. *elongatus;* Jacobson, 1906:267.

Adults

Diagnostic combination.— Distinguished from adults of *E. lapponicus obliteratus* by smaller size (elytral length (EL) of most specimens less than 5.4 mm).

Description.— Dorsal body surface black to brilliant green and copper. Elytral pits generally not clearly delineated. Frontal impression of head indistinct or clearly delineated. Pronotum with one pair of discal impressions. Elytral pits barely or clearly impressed; lateral ridges in pits either absent, suggested, or clearly delineated. Head wide and pronotum long (means of the following ratios were significantly different from those of *E. lapponicus obliteratus:* PW/HW less than 1.05, EL/HW less than 2.32, EW/HW less than 0.830, and PL/EL more than 0.39).

Integument sculpture. Puncture 20 microns in diameter on scutellum and all coxae, 25 to 30 microns in diameter on dorsal body surface and on thoracic sterna, and 30 to 40 microns in diameter on pleura and on lateral portion of abdominal sterna. Punctures 25 to 50 microns apart generally, but sparser on scutellum, elytron, medial portion of thoracic sterna, and coxae.

Microsculpture absent from or indistinctly outlined on scutellum and on base of mesosternum, convex on abdominal sterna, on elytron, and on metepisternum, and flat on remaining sclerites.

Table 1. Descriptive statistics for *E. lapponicus lapponicus*, based on 10 males and 10 females from mainland northwestern North America (Alaska, Yukon, North West Territories, Alberta, and British Columbia).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.65–1.97	1.85	0.140	0.043	5.0
PW	1.85–2.22	2.08	0.165	0.049	5.3
EL	4.20–5.10	4.68	0.375	0.113	5.4
HW	1.87–2.15	2.05	0.109	0.032	3.5
B. Proportions					
PL/PW	0.830–0.927	0.886	0.043	0.013	3.2
PL/EL	0.366–0.418	0.395	0.019	0.006	3.1
PL/EW	1.030–1.190	1.110	0.052	0.015	3.1
PL/HW	0.825–0.938	0.902	0.044	0.013	3.2
PW/EL	0.425–0.468	0.446	0.020	0.006	3.1
PW/EW	1.190–1.330	1.260	0.063	0.019	3.3
PW/HW	0.925–1.070	1.020	0.052	0.015	3.4
EL/EW	2.720–3.000	2.820	0.101	0.030	2.4
EL/HW	2.150–2.380	2.290	0.105	0.031	3.1
EW/HW	0.725–0.852	0.810	0.049	0.015	4.0

Male genitalia. Apex of median lobe in dorsal view with sharp point on right side near base of apical spatula (Fig. 40b), in lateral view spatula moderately expanded and slightly bent ventrally; both right and left paramere wide with short setae extended in apical 0.3 (Figs. 40c, 40d); internal sac as in Fig. 40a.

Measurements and proportions.— See Table 1.

Variation.— Two composite samples, one from Scandinavia and one from Alaska, were studied. In Scandinavia, adults are generally larger, the elytral sculpture is little impressed and the pronotum is relatively wide (mean of ratio PW/EL is significantly larger than means of the mainland North American sample). In North America the pronotum is relatively long (mean of ratio PL/PW is significantly larger than that of Scandinavian sample).

Third Instar Larvae

Diagnostic combination.— Head, pronotum and most of tergum (including base of urogomphi) orange.

Description.— Head (except for darker area near frontale), disc of pronotum and mesonotum, and most of tergum 9 including base of urogomphi orange; remainder dark brown and dull (preserved specimens tend to fade to brown). Prementum with less than three accessory setae dorso-laterally. Meshed microsculpture present on entire dorsal surface and latero-ventral surface of parietale, and on all of nota.

Note about description.— Luff (1976) described briefly the first and second instar larvae. I did not have access to these. I studied only a third instar larva collected by Lindroth. This specimen was very pale, thus for color I used descriptions by Lindroth (1954) and Luff (1976).

Geographical Distribution and Affinities, and Notes

Distribution.— This Holarctic subspecies lives in the subarctic regions, from northern British Isles to Kamchatka (Lindroth, 1945), and from Alaska to Labrador. For North American distribution see Fig. 157.

Collecting notes.— Adults are hygrophilous, and live near cold waters. The preferred substrate is of neutral PH where mosses of the genus *Paludella* and other short vegetation such as *Marchantia* grow. Exposure is sunny, though some small and scattered conifers are present in some sites. This type of habitat is found near springs, brooks and small ponds. Adults are mostly seen in spring, but occur sporadically also later in summer. Fully grown third instar larvae and teneral adults were collected in July in Labrador, thus adults probably overwinter. Adults probably fly as suggested by two specimens collected on the shore of Lesser Slave Lake, Alberta, in an atypical habitat.

Taxonomic notes.— See discussion under *E. lapponicus obliteratus*. I studied 80 adults and one third instar larva.

Elaphrus lapponicus obliteratus Mannerheim new status
Figs. 40a-d, 118, 131, 157

Elaphrus obliteratus Mannerheim, 1853:117. Type locality: Paul Harbour, Kodiak Island, Alaska; type in Zoological Museum, University, Helsinki; type seen by Lindroth (1961). Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Marseul, 1882:4. Lindroth, 1961:111.

Adults

Diagnostic combination.— Distinguished from adults of *E. lapponicus lapponicus* by their large size (elytral length (EL) mostly more than 5.5 mm).

Description.— As in *E. lapponicus lapponicus* except as follows. Head narrow and pronotum short (means of the following ratios were significantly different from those of *E. lapponicus lapponicus:* PW/HW greater than 1.058, EL/HW more than 2.36, EW/HW more than 0.846 and PL/EL less than 0.386).

Variation.— See Table 2 and discussion under *E. lapponicus lapponicus*.

Distribution.— Known from a few localities in the United States. ALASKA: Kodiak Island: Bare Lake (10; UASM, MCZC), Pinguicula Lake (12; UASM, MCZC), R.A. (Russian America) (1;BMNH).

Collecting notes.— Lindroth (1969b) and Ball (pers. comm.) reported specimens of this subspecies as abundant in sphagnum bogs.

Taxonomic notes.— Adults of many species of ground beetles are larger and brighter in regions with cool or cold maritime climate than elsewhere (Lindroth, 1955 and 1961). Adults of *E. lapponicus* are also larger in these regions (Norway, coastal mainland Alaska, Labrador and Kodiak). However, those from Kodiak are much larger than expected. My interest in them arose when G.E. Ball noted that he collected them on sphagnum moss, which is a habitat avoided by the mainland specimens.

I also studied ratios derived from measurements. Both samples from Scandinavia and western North America differ significantly from those of Kodiak in means of six ratios. These ratios were tested in relation to body size for correlation. Within each sample, there seems to be little or no correlation with size. However, there is a weak correlation with size between samples for ratios PW/HW and EW/HW. Mainland specimens differ significantly from the Kodiak sample in means of two ratios PL/EL and EL/HW. The Norway sample is significantly different from the Kodiak sample in the mean of ratio PW/EL, and from mainland North American sample in the mean of ratio PL/PW. Scandinavian and North American sample differ significantly from each other in the mean of ratios PW/EL and PL/PW.

Table 2. Descriptive statistics for *E. l. obliteratus*, based on 12 males and eight females from Pinguicula Lake and Bare Lake, both localities on Kodiak Island, Alaska.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.00–2.32	2.20	0.121	0.036	3.7
PW	2.40–2.72	2.56	0.125	0.037	3.2
EL	5.15–6.20	5.75	0.359	0.107	4.2
EW	1.90–2.20	2.04	0.133	0.038	4.3
HW	2.25–2.52	2.39	0.105	0.031	2.9
B. Proportions					
PL/PW	0.818–0.880	0.857	0.026	0.008	2.0
PL/EL	0.364–0.395	0.382	0.013	0.004	2.3
PL/EW	1.040–1.130	1.070	0.040	0.012	2.5
PL/HW	0.874–0.968	0.918	0.034	0.010	2.5
PW/EL	0.421–0.471	0.446	0.019	0.006	2.8
PW/EW	1.200–1.320	1.250	0.051	0.015	2.7
PW/HW	1.030–1.130	1.070	0.041	0.012	2.5
EL/EW	2.680–2.950	2.810	0.114	0.034	2.7
EL/HW	2.280–2.550	2.400	0.117	0.035	3.3
EW/HW	0.809–0.903	0.857	0.037	0.011	2.9

As observed in many other carabid species common to both regions, slight differences between North American and Scandinavian populations are expected. Despite the great geographical gap between both samples, they are essentially the same, except for the narrower pronotum in specimens from North America. However, differences between above samples and that of Kodiak suggest lack of gene flow over a long period, and the independant evolution of the Kodiak population. Habitat differences, significant difference in means of ratios PL/EL and EL/HW, and large size (taxonomically significant) justify ranking the allopatric Kodiak population as a distinct subspecies.

Lindroth (1969b: 195-210) in his account of the Kodiak carabid fauna found no evidence of endemic species or races. However, he felt that some carabid species existed in this refugium during at least the last glaciation because of the higher proportion of micropterous species than on nearby coastal regions of Alaska. A postglacial recolonization, he assumed, would have produced a higher proportion of macropterous individuals. Ball (1969) studied six micropterous species of *Pterostichus* in the subgenus *Cryobius*. He found that three were not different from nearby Kenai Peninsula. Of remaining species, *P. parasimilis* Ball differed slightly in color, and *P. pinguedineus* Eschscholtz and *P. riparius* Dejean showed longer elytra (means for each sex were significantly different) than those of populations from other coastal Alaskan localities. However, he found no differences in ratios or in behaviour. Moreover, Smetana (1971) described the Kodiak population of the staphylinid *Quedius labradorensis* Smetana, characterized by longer size and relatively wider pronotum, as an endemic subspecies *Q. labradorensis insularis*. Thus, there is evidence for the existence of a refugium on Kodiak Island during the last glacial period as shown by structural differences in adults of some species

of beetles occuring both on the island and on the mainland. Since specimens of *E. lapponicus* tolerate cold, I feel that these beetles survived in the refugium through one or more glacial periods when selection was probably intensive.

Subgenus *Neoelaphrus* Hatch

Neoelaphrus Hatch, 1951:113. Type-species: *Elaphrus uliginosus* Fabricius, 1792, fixed by Hatch (1951), by original designation. Hatch, 1953:63. Ball, 1960:106. Lindroth, 1961:112. Nakane, et al. 1963:18.

Elaphrus; Semenov, 1895:309 *(ex parte)*. Jacobson, 1906:267 *(ex parte)*. Reitter, 1908:96, 97 *(ex parte)*. 1909:104 *(ex parte)*. Bänninger, 1919:149 *(ex parte)*. Porta, 1923:78. Semenov, 1926:39. Portevin, 1929:41. Jeannel, 1941:216.

Adults

Diagnostic combination.— Distinguished from adults of other subgenera as in following. Hind coxa and hind femur respectively with less than six setae. Prosternum without setae on disc. Suture between proepisternum and proepimeron sharply delineated.

Description.— *Head.* Frons with medial fovea, in some species with additional smaller foveae posteriorly. Clypeus with one pair of setae. Terebral margin of right mandible less than 0.5 as long as mandible; basal retinacular tooth emarginate; apex of retinacular tooth situated anteriad of terebral tooth. Maxillary palpomere 3, 0.3 to 0.4 as long as palpomere 4. Galeomere 1, 1.5 as long as maxillary palpomere 2.

Thorax. Lateral margin of pronotum completely beaded or unbeaded. Fringe of setae on posterior margin of pronotum ended before hind angles; setae scimitar-shaped and narrow. Suture between proepisternum and proepimeron sharply delineated. Prosternum asetose on disc, but setose on process. Process of mesosternum asetose; postero-lateral ridge of mesosternum absent or weakly outlined.

Abdomen. Tergum 7 with setae along anterior margin or on entire surface.

Elytra. Striae lacking or suggested at base. Transverse basal stria sharply outlined at shoulder. Setigerous punctures of elytron 40 to 50 microns in diameter. Mirrors of similar width in interval 3. Elytral pits with fewer than 30 irregularly distributed punctures (Figs. 132 to 134).

Legs. Foreleg: trochanter with one or two setae; femur with 32 to 57 setae; tibia with 19 to 25 setae; inner dorsal fringe 0.6 as long as tibia, and without setae posteriorly; first four tarsomeres of males with ventral spongy pubescence. Midleg: trochanter with one or two setae; femur with 27 to 58 setae; tibia with 56 to 80 setae. Hindleg: coxa with three to six setae on inner half of process; femur with five to 11 setae; tibia with 51 to 80 setae.

Male genitalia. Internal sac of median lobe with large scales posteriorly.

Ovipositor. Basal sclerite of stylus with numerous very small setae apico-ventrally; apical sclerite with few stout setae on dorso-lateral and dorso-medial ridges, apex of sclerite with one very small seta or in some species with one more extemely small seta (Fig. 73).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other subgenera as in following. Epicranial suture 0.8 to 1.2 as long as scape (Fig. 90a). Ventral surface of stipes thickly sclerotized, and two posterior pores distant (Fig. 85b).

First Instar Larvae

Description.— Medial point of nasale obtuse; teeth of nasale absent or large and ending subapically on medial point (Fig. 90b). Epicranial suture 0.8 to 1.2 as long as antennal scape. Head elongate: bisinuation of lateral margin behind eye with anterior convexity longer than posterior one (Fig. 90a). Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 110 to 130°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale equilateral. Stipes entirely sclerotized ventrally; lateral margin entire; dorsal surface with about 30 setae on inner half, subapical setae roughly distributed in one row; two postero-ventral pores distant (Fig. 85b).

Second Instar Larvae

Description.— Outer margin of stipes entire. Each sclerite of mesonotum with about 15 accessory setae. Each sclerite of terga 1 to 8 with 16 to 36 accessory setae. Basal major accessory setae on urogomphus postero-lateral; microsculpture on urogomphus barely suggested or scale-like. Pointed microsculpture absent from anterior band of terga 1

to 8, present on (10% of surface) or absent from anterior band of tergum 9, and present on (5% of surface) or absent from posterior band. Hypopleuron of abdominal segments 1 to 8 with eight to 20 accessory setae.

Third Instar Larvae

Description.— Prementum with about six accessory setae dorso-laterally. Proepisternum with 25 accessory setae. Larges projection of urogomphus in lateral view medium-sized or large (Figs. 98c, 99b). Each sclerite of terga 1 to 8 with 35 to 140 accessory setae. Epipleuron of abdominal segments 2 to 8 with 17 to 60 accessory setae. Hypopleuron of abdominal segments 1 to 8 each with 14 to 47 accessory setae. Sternite of abdominal segment 1 with four to 12 accessory setae, those of segments 2 to 7 each with 18 to 24, that of segment 8 with 18 to 38, that of segment 9 with two to eight, and that of segment 10 with six to 12.

Geographical Distribution and Affinities, and Notes

Distribution.— The ranges of species of this subgenus extend across Palaearctic and Nearctic regions, from the subarctic to the temperate zones.

Taxonomic notes.— Species of this subgenus are arranged in three species groups: the *uliginosus* group, the *fuliginosus* group and the *cupreus* group. Each group is characterized in the key as well as in the text. My main reasons for giving formal recognition to these three monophyletic groups were zoogeographical. The *uliginosus* group is restricted to the Palaearctic region, the *fuliginosus* group is restricted to the eastern Nearctic region, and the *cupreus* group has two lineages of which one is Palaearctic and the other Nearctic.

Key to species of subgenus *Neoelaphrus* Hatch

Adults

1 Fringe of setae on posterior margin of pronotum ending 40 to 120 microns from postero-lateral angles (Fig. 17a). Lateral margin of pronotum in lateral view sinuate near middle, pronotal epipleuron narrowest at this point (Fig. 17b). Bead of pronotal lateral margin 20 to 30 microns in width. Pronotum with one antero-submedial impression (indistinct in individuals of *E. splendidus*). Palaearctic Region 2

1′ Fringe of setae on posterior margin of pronotum ending 150 to 250 microns from postero-lateral angles (Figs. 18a and 19). Lateral margin of pronotum in lateral view not sinuate near middle, pronotal epipleuron equally narrow from middle to anterior margin (Fig. 18b). Bead of pronotal lateral margin either absent, 10 to 15 microns in width, or 20 to 30 microns in width. Pronotum without antero-submedial impression 6

2 (1) Elytron with four rows of sharply outlined and subconvex mirrors on intervals 3, 5, 7 and 9. Upper surface of body including elytral pits brilliant metallic golden green. Pronotum without or with suggested antero-submedial impressions on each side. Punctures 30 to 40 microns in diameter, on elytral intervals 4, 6 and 8, and 20 to 25 microns in diameter on head and pronotum. Eastern Siberia ..... *E. splendidus* Fisher von Waldheim p. 254

2′ Elytron with one or two rows of sharply outlined and flat mirrors on intervals 3, or 3 and 5. Upper surface of body not brilliant green, (except in *E. pyrenoeus*); elytral pits purple, or if green, then elytral surface brown-copper. Pronotum with clearly defined antero-submedial

impressions. Punctures 20 to 25 microns in diameter on head, pronotum and elytral intervals, 4, 6 and 8 3

3 (2′) Punctures 100 to 150 microns apart on intervals 4, 6 and 8. Lateral ridges of elytral pits convex and wide (Fig. 132). Northern Japan and adjacent regions of USSR ..... *E. japonicus* Uéno p. 254

3′ Punctures 30 to 40 microns apart on invervals 4, 6 and 8. Lateral ridges of elytral pits weakly convex, narrow or absent (Figs. 119 an 120) 4

4 (3′) Dorsal surface of body bright brown-copper. Elytral pits metallic green. Kansu, China ..... *E. potanini* Semenov p. 259

4′ Dorsal surface of body dark, or brilliant green or brilliant brown-copper in few specimens. Elytral pits purple 5

5 (4′) Dorsal surface of body dark green or copper (some individuals brilliant). Intervals 4, 6 and 8 subcostate (except specimens from central Asia). Meshes of microsculpture clearly outlined on elytron (Fig. 137). Elytral pits slightly impressed (Fig. 119). Europe east to Yenisey River and western China ..... *E. uliginosus* Fabricius p. 255

5′ Dorsal surface of body brilliant green-olive or brown-copper. Intervals 4, 6 and 8 not costate. Meshes of microsculpture absent from elytron except near shoulder, elytral pits and postero-lateral impressions of pronotum (Fig. 138). Elytral pits deeply impressed (Fig. 120). Southern Spain to Pyrénées ..... *E. pyrenoeus* Motschulsky p. 258

6 (1′) Lateral margin of pronotum unbeaded or beaded; bead, when present, 20 to 30 microns in width. Punctures of pleura and lateral portion of abdominal sterna 30 to 45 microns in diameter; punctures apparently larger (about 80 microns in diameter) because of widely depressed area around each puncture–best seen on proepisternum (Fig. 107). Abdominal sterna 5 and 6 each with fewer than three accessory setae medially (Fig. 139). Tibia of foreleg of male with large projection at base of posterior spur and with small projection at base of apical spur–best seen in posterior view (Fig. 149). Eastern Nearctic Region 7

6′ Lateral margin of pronotum beaded, bead 10 to 15 microns in width. Punctures of pleura and lateral portion of abdominal sterna 20 to 35 microns; area around each puncture narrowly or not depressed (Fig. 108). Abdominal sterna 5 and 6 each with five to 15 accessory setae, or accessory setae lacking then punctures of ventral body surface 20 to 25 microns apart. Tibia of foreleg of male without projection at base of both spurs (cuticle at base of posterior spur in some specimens sharp but not projected 9

7 (6) Dorsal body surface dark green. Lateral margin of pronotum beaded; bead 20 to 30 microns in width. Dorsal surface of tibia and tarsomeres metallic green. Abdominal sternum 7 of males with 10 to 20 accessory setae .....
..... *E. fuliginosus* Say p. 260

7′ Dorsal body surface dark copper or brass-silver. Lateral margin of pronotum not beaded (Fig. 107). Dorsal surface of tibia and tarsomeres metallic purple. Abdominal sternum 7 of males without accessory setae (Fig. 139) 8

8 (7′) Dorsal body surface nearly black with copper hue. Antennomeres 1 to 3 black. Lateral ridges of elytral pits convex and wide (Fig. 132). Elytral mirrors present on intervals 3 and 5; mirrors little contrasted against dark background color of intervals 2, 4 and 6. Trochanter of foreleg with one seta (Fig. 145). Punctures of dorsal body surface 10 to 200 microns apart ..... *E. cicatricosus* LeConte p. 262

8′ Dorsal body surface brass-silver. Antennomeres 1 to 3 reddish brown. Lateral ridges of elytral pits suggested or absent (Fig. 121). Elytral mirrors present on interval 3 only; mirrors sharply contrasted against silver background of intervals 2 and 4. Trochanter of foreleg with two setae. Punctures of dorsal body surface 10 to 30 microns apart on head and on elytral intervals 4, 6 and 8, and 20 to 40 microns on pronotum (Figs. 104 and 121) ..... *E. lindrothi* new species p. 264

9 (6′) Lateral ridges of elytral pits wide and not fused anteriorly or posteriorly (Fig. 132). Elytral mirrors contrasting against duller intervals 2, 4 and 6. Microsculpture flat or subconvex on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 132). Palaearctic Region 10

9′ Lateral ridges of elytral pits distinclty fused anteriorly and posteriorly or indistinctly so (then ridges narrow) (Figs. 133 and 134). Elytral mirrors weakly contrasted against brilliant intervals 2, 4, 6 and 8. Microsculpture absent or suggested in spots on head, pronotum and intervals 4, 6 and 8 (Figs. 133 and 134). Nearctic Region 11

10 (9) Tarsomeres and apex of tibiae metallic green dorsally; dorsal body surface greenish with bright green pronotal and head impressions. Punctures of dorsal body surface dense: punctures three to ten microns apart and polygonal near anterior angles of frons at level of clypeal setae, 30 to 50 microns apart on disc of pronotum and elytral intervals 4, 6 and 8, and space between suture and first pit of interval 3 with three to four rows of punctures; punctures 25 to 30 microns in diameter on clypeus, and 25 to 35 microns in diameter near antero-lateral angles of frons. Eastern Palaearctic Region ..... *E. sibiricus* Motschulsky p. 266

10′ Tarsomeres and apex of tibiae purple; dorsal body surface dark copper with blue-green pronotal and head impressions. Punctures of dorsal body surface sparse: punctures 10 to 30 microns apart and round near anterior angles of frons at level of clypeal setae, 50 to 100 microns apart on disc of pronotum and elytral intervals 4, 6 and 8, and space between suture and first pit of interval 3 with one or two rows of punctures; punctures 15 to 20 microns in diameter on clypeus and near antero-lateral angles of frons. Palaearctic Region ..... *E. cupreus* Duftschmid p. 268

11 (9′) Punctures 10 to 100 microns apart on pleura and laterally on basal abdominal sterna. Male tibia of midleg with sharp projection at base of inner spur (Fig. 150). Punctures of elytral intervals 4, 6 and 8, 30 to 120 microns apart (Fig. 122) ..... *E. clairvillei* Kirby p. 271

11′ Punctures 10 to 20 microns apart on pleura, and laterally on basal abdominal sterna. Male tibia of midleg without projection at base of inner spur. Punctures of elytral intervals 4, 6 and 8, either 10 to 20 microns

apart, or more than 200 microns apart 12

12 (11′) Dorsal body surface olive, blue-green, dark brown-olive, or red-brown; dorsal surface of tibia and tarsomeres metallic green or copper; antennomeres 1 to 3 brown. Pronotum with two submedial impressions. Lateral ridges of elytral pits narrow and weakly convex (Fig. 134). Punctures 15 to 20 microns apart on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123). Abdominal sterna 5, 6 and 7 each without or with fewer than three accessory setae. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada .....
..... *E. olivaceus* LeConte p. 276

12′ Dorsal body surface brilliant black; dorsal surface of tibia and tarsomeres metallic purple; antennomeres 1 to 3 black. Pronotum with one submedial impression. Lateral ridges of elytral pits wide and convex (Fig. 133). Punctures about 60 microns apart on head, 10 to 200 microns apart on pronotum and 200 microns apart on elytra. Abdominal sterna 5, 6 and 7 with five to 20 accessory setae. California to westernmost Nevada .....
..... *E. laevigatus* LeConte p. 280

First Instar Larvae

1 Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on less than 3% of parietale. Eastern Nearctic Region 2

1′ Epicranial suture subequal or longer than outer sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on 5% or more of parietale 4

2 (1) Parietale mostly dark except behind eyes. Pointed microsculpture present near suture of mesonotum and metanotum .....
..... *E. lindrothi* new species p. 264

2′ Parietale mostly pale except near suture of parietale and base of antennae. Pointed microsculpture absent from sutural portion of mesonotum and metanotum 3

3 (2′) Nasale with teeth. Pointed microsculpture present ventro-laterally on 3% of parietale. Darker pattern on dorsal surface of parietale extended along occipital suture. Pointed microsculpture present on entire surface of abdominal sternite 10 ..... *E. fuliginosus* Say p. 260

3′ Nasale without teeth. Pointed microsculpture absent from ventro-lateral surface of parietale. Darker pattern on dorsal surface of parietale not extended to occipital suture. Pointed microsculpture absent from abdominal sternite 10 ..... *E. cicatricosus* LeConte p. 262

4 (1′) Meshes of microsculpture absent from pronotum 5

4′ Meshes of microsculpture present on 5% or more of pronotum 6

5 (4) Meshes of microsculpture of parietale restricted baso-laterally (5 to 10% of dorsal surface); pointed microsculpture of parietale restricted baso-laterally (5% of dorsal and ventral surface). Palaearctic Region .....
..... *E. cupreus* Duftschmid p. 268

5′ Meshes of microsculpture of parietale widespread baso-laterally (20% of dorsal surface); pointed microsculpture of parietale widespread baso-laterally (10% of dorsal surface and 2% of ventral surface). Nearctic Region ..... *E. clairvillei* Kirby p. 271

6 (4′) Pointed microsculpture of parietale restricted baso-laterally (5% of dorsal surface and 3% of ventral surface). Seta AII-E of pronotum medium-sized. Pointed microsculpture of mesonotum and metanotum widespread near suture (20% of surface) restricted laterally (5% of surface), and absent from posterior band. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276

6′ Pointed microsculpture of parietale widespread baso-laterally (50% of dorsal surface and 15% of ventral surface). Seta AII-E of pronotum large. Pointed microsculpture of mesonotum and metanotum restricted near suture (10% of surface) and widespread laterally (35% of surface), and present on posterior band (60% of surface). California and westernmost Nevada ..... *E. laevigatus* LeConte p. 280

Second Instar Larvae

1 Dorsal surface of parietale mostly pale, dark only near frontale and base of antennae. Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture absent from dorso-lateral surface of parietale. Urogomphus with nine or more accessory setae. Eastern Nearctic Region 2

1′ Dorsal surface of parietale mostly dark, pale behind eyes and/or base. Epicranial suture subequal or longer than outer sclerotized margin of antennomere 1. Pointed microsculpture present baso-laterally on parietale (15% or more of dorsal surface). Urogomphus with less than nine accessory setae 4

2 (1) Microsculpture present over mesonotum and metanotum; pointed microsculpture well developed near suture ..... *E. lindrothi* new species p. 264

2′ Microsculpture absent from mesonotum and metanotum, or if present, then pointed microsculpture absent near suture 3

3 (2′) Sclerites moderately setose: pronotal epipleuron with one or two accessory setae, urogomphus of tergum 9 with about 14 accessory setae (Fig. 98b). Meshes of microsculpture clearly outlined on nota, terga and urogomphi ..... *E. fuliginosus* Say p. 260

3′ Sclerites densely setose: pronotal epipleuron with seven accessory setae, urogomphus of tergum 9 with about 25 accessory setae (Fig. 99a). Meshes of microsculpture absent from nota, very restricted on terga, and suggested on urogomphi ..... *E. cicatricosus* LeConte p. 262

4 (1′) Pointed microsculpture present near suture of mesonotum (2% of surface) and of metanotum (10% of surface), on lateral portion of mesonotum and

metanotum (15% of surface), and on anterior band of tergum 9 (10% of surface) 4

4′ Pointed microsculpture absent from sutural portion of mesonotum and metanotum, absent from or present on lateral portion of both nota (10% of surface), and absent from anterior band of tergum 9 6

5 (4) Pointed microsculpture of membrane on ventral surface of abdomen not extending to sternites 2 to 7. Meshes of microsculpture absent or indistinctly outlined on 50% of disc of pronotum. Palaearctic Region ..... *E. cupreus* Duftschmid p. 268

5′ Pointed microsculpture of membrane on ventral surface of abdomen extending to sternites 2 to 7. Meshes of microsculpture clearly outlined on 10% of disc of pronotum. Nearctic Region ..... *E. clairvillei* Kirby p. 271

6 (4′) Pointed microsculpture of parietale moderately widespread baso-laterally (15% of dorsal surface and 3% of ventral surface). Meshes of microsculpture moderately widespread on pronotum (30% of surface), and on mesonotum and metanotum (40% of surface). Pointed microsculpture absent from lateral portion of nota. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276

6′ Pointed microsculpture of parietale widespread baso-laterally (30% of dorsal surface and 10% of ventral surface). Meshes of microsculpture widespread on pronotum (75% of surface) and on mesonotum and metanotum (90% of surface). Pointed microsculpture present from lateral portion of mesonotum and metanotum (10% of surface). California or westernmost Nevada ..... *E. laevigatus* LeConte p. 280

Third Instar Larvae

1 Dorsal surface of parietale mostly pale, dark only near frontale and base of antennae. Epicranial suture subequal to inner sclerotized margin of antennomere 1. Pointed microsculpture absent from dorsal surface of parietale. Urogomphus with nine or more accessory setae. Eastern Nearctic Region 2

1′ Dorsal surface of parietale mostly dark, pale behind eyes and/or base. Epicranial suture subequal or longer than outer margin of antennomere 1. Pointed microsculpture moderately widespread on parietale (15% of dorsal surface). Urogomphus with less than nine accessory setae 4

2 (1) Mesonotum and metanotum with pointed microsculpture near suture. Mesonotal and metanotal epipleuron with one to five accessory setae ..... *E. lindrothi* new species p. 264

2′ Mesonotum and metanotum without pointed microsculpture near suture. Mesonotal and metanotal epipleuron without or with five to 15 accessory setae 3

3 (2′) Sclerites moderately setose: posterior band of mesonotum and metanotum without acessory setae, urogomphus with nine to 14 accessory setae (Fig. 98c). Meshes of microsculpture clearly outlined over most of nota and

terga ..... *E. fuliginosus* Say p. 260

3′ Sclerites densely setose: posterior band of mesonotum and metanotum with five to 15 accessory setae laterally, urogomphus with about 30 accessory setae (Fig. 99b). Meshes of microsculpture absent from nota and very restricted on terga ..... *E. cicatricosus* Leconte p. 262

4 (1′) Meshes of microsculpture absent from disc of pronotum. Pointed microsculpture present on lateral portion of mesonotum and metanotum (10% of surface), and on anterior band of tergum 9 (60% of band surface). Abdominal sternite 9 with about six accessory setae. Pointed microsculpture present on posterior band of terga 1 to 8 (5% or more of surface) 5

4′ Meshes of microsculpture present on pronotum (10% or more of surface). Pointed microsculpture absent from mesonotum, metanotum, and anterior band of tergum 9. Abdominal sternite 9 with two accessory setae. Pointed microsculpture absent from posterior band of terga 1 to 8. Nearctic Region 6

5 (4) Pointed microsculpture absent from sutural area of mesonotum, present on metanotum (3% of surface). Palaearctic Region ..... *E. cupreus* Duftschmid, p. 268

5′ Pointed microsculpture near suture on 10% of disc of mesonotum and metanotum. Nearctic Region ..... *E. clairvillei* Kirby p. 271

6 (4′) Meshes of microsculpture restricted: 10% of pronotum, and 40% of mesonotum and metanotum. Pointed microsculpture absent from anterior band of terga 1 to 8. Central British Columbia east to Atlantic coast of northern United States and adjacent Canada ..... *E. olivaceus* LeConte p. 276

6′ Meshes of microsculpture widespread: 75% of pronotum, and on 90 to 100% of mesonotum and metanotum. Pointed microsculpture present on 5% or more of anterior band of terga 1 to 8. California to westernmost Nevada ..... *E. laevigatus* LeConte p. 280

THE *ULIGINOSUS* GROUP

Adults

Diagnostic combination.— Fringe of setae on posterior margin of pronotum terminated near middle of postero-lateral impression or nearer hind angle (Fig. 17a); lateral margin of pronotum wide, depressed in lateral view, pronotal epipleuron narrowest near middle (Fig. 17b); bead of lateral margin of pronotum 20 to 30 microns in width. Tibia of foreleg in males without projection at base of apical and posterior spur. Punctures of proepisternum 25 to 30 microns in diameter, and surrounding surface not impressed.

The five species of this group are restricted to the temperate and boreal areas of the Palaearctic Region. Larvae of species of this group are not known.

Elaphrus splendidus Fischer von Waldheim
Fig. 41a-d

Elaphrus splendidus Fischer von Waldheim; 1828:267. Type area: Mongolia: type not seen. Motschulsky, 1846:71. Solsky, 1872:233. Marseul, 1880:29. 1882:4. Jacobson, 1906:267. Bänniger, 1919:147.
Elaphrus splendidulus Motschulsky, 1850b:LXVII. New Synonym.

Adults

Diagnostic combination.— Distinguished from adults of other species of group by brilliant green color on dorsal body surface, and by four rows of sharply outlined mirrors on the elytron.

Description.— Dorsal body surface (including pits) brilliant metallic green except for brilliant black mirrors; ventral surface dark metallic golden green; appendages black except femora with metallic green hue. Pronotum without small impressions antero-laterally. Elytral pits shallowly impressed, lateral ridges narrowly outlined or absent. Mirrors clearly outlined on intervals 3, 5, 7 and 9.

Integument sculpture. Punctures 30 to 40 microns in diameter on ventral body surface and on elytral intervals 4, 6 and 8, and 20 to 25 microns in diameter on pronotum and head. Distribution of punctures as in that of *E. uliginosus* but punctures denser on intervals 4, 6 and 8.

Microsculpture absent from or indistinctly outlined on intervals 4, 6 and 8, absent from or present in spots on pronotum.

Male genitalia. Apex of median lobe in dorsal view not twisted, thin-edged (30 microns in width) (Fig. 41a), in lateral view with apex slightly enlarged as in *E. uliginosus* but relatively wider (Fig. 41b).

Measurements and proportions.— Based on four specimens from Omsulcschan in northeastern Siberia. PL, 1.8-1.94-2.0 mm; 2.1-2.33-2.4 mm; EL, 4.6-4.98-5.1 mm; EW, 1.7-1.8-1.9 mm; HW, 2.0-2.11-2.2 mm; PL/PW 0.816-0.834-0.854; PL/EL, 0.385-0.389-0.398; PL/EW, 1.05-1.08-1.12; PL/HW, 0.867-0.920-1.0; PW/EL, 0.462-0.467-0.476; PW/EW, 1.28-1.29-1.32; PW/HW, 1.04-1.10-1.17; EL/EW, 2.71-2.77-2.82; EL/HW, 2.24-2.36-2.51; EW/HW, 0.807-0.852-0.890.

Distribution.— Kryzhanovskij (*in litt.*) reported adults of this species from Mongolia (Khentei Mts.) and Eastern Siberia to Kamchatka (from Irkutsk to Amur and Ussuri Rivers, Kamchatka, and Commander Is.).

Taxonomic notes.— Motschulsky's name was created by accidentally modifying Fischer's name and describing the species briefly. This made the name valid.

I have seen four specimens from Omsulcschan in northeastern Siberia, and dissected the only male.

Geographical affinities.— The range of this species overlaps with that of *E. sibiricus* and perhaps with that of *E. cupreus*.

Elaphrus japonicus Uéno
Fig. 42a-b

Elaphrus cupreus Habu; 1953:19 (*In*: Uéno, 1954) (*nec* Duftschmidt, 1812:194).
Elaphrus sibiricus Uéno; 1953:51 (*In*: Uéno, 1954) (*nec* Motschulsky, 1846:71).
Elaphrus japonicus Uéno, 1954:718. Type locality: Takinomata, Takedate, Aomori Prefecture, Japan; type not seen. Nakane, et. al., 1963:18. Ohkura, 1973:5.

Adults

Diagnostic combination.— Distinguished from adults of other species of group by scattered punctures on dorsal body surface (100 to 150 microns apart on intervals 4, 6 and 8), and by dark brown dorsal surface of body with copper reflections.

Description.— Dorsal body surface dark brown with copper luster except for purple pits; ventral body surface black with metallic golden hue; tibiae piceous and tarsomeres dark blue dorsally.

Impressions of pronotum numerous, as in *E. uliginosus*. Pits of elytra deeply impressed, lateral ridges wide and prominent. Elytral mirrors sharply outlined and slightly contrasted in intervals 3 and 5.

Integument sculpture. Punctures 20 to 25 microns in diameter on dorsal body surface, and 30 to 40 microns in diameter on ventral body surface. Punctures on dorsal body surface scattered: 100 to 150 microns apart on intervals 4, 6 and 8.

Microsculpture flat, over most of surface of body.

Male genitalia. Apex of median lobe in dorsal view (Fig. 42a) straight, thin-edged (30 microns in width), in lateral view with apex enlarged ventrally (Fig. 42b).

Measurements and proportions.— Based on two specimens from Aomori Pref., Japan. PL, 1.8-1.9 mm; PW, 2.1-2.3 mm; EL, 4.6-4.9 mm; EW, 1.7-1.8 mm; HW, 2.2-2.3 mm; PL/PW, 0.835-0.847; PL/EL, 0.388-0.391; PL/EW, 1.04-1.07; PL/HW, 0.828-0.835; PW/EL, 0.462-0.464; PW/EW, 1.25-1.27; PW/HW, 0.977-1.000; EL/EW, 2.68-2.75; EL/HW, 2.11-2.15; EW/HW, 0.770-0.802.

Distribution.— Adults are reported from Honshu Island, Japan and the Soviet far east (Kryzhanouskij, *in litt.*) from Middle Amur and Khabarousk to Vladivostok. I have seen specimens from Takedate-mura, Aomori Pref. (UASM, HGou).

Taxonomic notes.— I studied and dissected two males.

Geographical affinities.— The ranges of this species and *E. splendidus* probably overlap.

Elaphrus uliginosus Fabricius
Figs. 17a-b, 43a-b, 119, 137

Elaphrus uliginosus Fabricius, 1792:178. Type locality: Germany; type not seen (see "Taxonomic notes"). Fabricius, 1801:245. Latreille, 1806:227. Gyllenhal, 1810:6. Dejean, 1826:269. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Küster, 1846:7. Letzner, 1849:50. Fairmaire and Laboulbène, 1854:6. Schaum, 1856:70. Stierlin, 1869:10. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Marseul, 1880:30. Sahlberg, 1880:10. Bedel, 1881:23. Fauvel, 1882:82. Marseul, 1882:4. Redtenbacher, 1874:6. Seidlitz, 1891:19. Ganglbauer, 1892:123. Semenov, 1895:312. Everts, 1898:49. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhnt, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Obenberger, 1917:9. Porta, 1923:78. Louvet, 1925:17, 20. Portevin, 1929:41. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:218. Lindroth, 1974:33.

Elaphrus riparius Olivier, 1790:4. Rossi, 1790:193. Geoffroy, 1799: 156 *(ex parte)*. Latreille, 1804:217. 1806:227. Gyllenhal, 1810:6.1827:397. *nec* Linnaeus, 1758.

Elaphrus latithorax Schönherr, (*In:* Dejean, 1826). Dejean, 1826:270. Semenov, 1895:312. NOMEN NUDUM.

Elaphrus impressifrons Chaudoir, 1842:815. Type locality: Lac Ladoga, Baschkiria, USSR; type not seen. Motschulsky, 1850a:5. Marseul, 1882:4. Semenov, 1895:312. Jacobson, 1906:267.

Elaphrus italicus Dalla-Torre, 1877:23. Type locality: Italy; type not seen. Semenov, 1895:312. Jacobson, 1906:267.

Elaphrus uliginosus var. *italicus;* Schilsky, 1889:194.

Elaphrus uliginosus purkynei Obenberger, 1917:9. Type locality: Cepelare, Bulgaria; type not seen. Louvet, 1925:20.

Elaphrus uliginosus laevisculptus Bänninger, 1919:147. Type locality: Tien-shan; type not seen. Louvet, 1925:20.

Elaphrus cupreus laevisculptus Reitter (*In*: Bänninger, 1919). NOMEN NUDUM.

Elaphrus bedeli Méquignon, 1924:127. Type locality: Scalas, France; type not seen. Louvet, 1925:20. Jeannel, 1941:218.

Elaphrus viridicupreus Louvet, 1925:18. Type locality: Sedan, France; type not seen. Jeannel, 1941:218.

Adults

Diagnostic combination.— Distinguished from adults of *E. pyrenoeus*, by dark green or copper dorsal surface of body, by sharply outlined meshes of microsculpture on intervals 4, 6 and 8. (Fig. 137) and by moderately impressed elytral pits (Fig. 119). Distinguished from remaining species of group by characters in key.

Description.— Dorsal body surface dark green or copper, rarely brilliant green, elytral pits purple; ventral body surface with dark metallic green or blue reflections; legs dark purple except for dark golden green femora.

Pronotum with postero-submedial impression in most specimens, and with two small impressions antero-lateral to main submedial impression. Elytral pits slightly impressed or not, lateral ridges clearly outlined except for specimens from western Himalaya. Mirrors sharply outlined and flat in interval 3, indistinctly outlined in intervals 7 and 9. Intervals 4, 6 and 8 in most specimens subcostate.

Table 3. Descriptive statistics for *E. uliginosus* based on 10 males and 10 females from central France and Switzerland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.4	2.08	0.185	0.054	5.8
PW	2.2–2.6	2.41	0.205	0.061	5.7
EL	4.7–5.5	5.10	0.381	0.114	5.0
EW	1.7–2.1	1.87	0.167	0.050	5.9
HW	2.2–2.6	2.33	0.164	0.049	4.7
B. Proportions					
PL/PW	0.816–0.888	0.864	0.030	0.009	2.3
PL/EL	0.381–0.427	0.409	0.019	0.006	3.2
PL/EW	1.050–1.170	1.110	0.056	0.017	3.4
PL/HW	0.833–0.938	0.894	0.040	0.012	2.9
PW/EL	0.446–0.500	0.474	0.019	0.006	2.7
PW/EW	1.240–1.350	1.290	0.057	0.017	3.0
PW/HW	0.989–1.090	1.030	0.049	0.015	3.2
EL/EW	2.570–2.830	2.720	0.105	0.031	2.6
EL/HW	2.100–2.310	2.190	0.086	0.026	2.6
EW/HW	0.750–0.856	0.804	0.039	0.012	3.3

Integument sculpture. Punctures 20 to 25 microns in diameter on head, on pronotum and on elytral intervals, and 30 to 40 microns in diameter on thoracic pleura and abdominal sterna. Punctures 30 to 40 microns apart on elytral intervals 4, 6 and 8, and on thoracic pleura; punctures of proepisternum 30 to 40 microns apart.

Microsculpture flat on dorsal surface except on mirrors, and convex in elytral pits and near postero-lateral angles of pronotum.

Male genitalia. Apex of median lobe in dorsal view twisted (Fig. 43a), thick-edged (65 microns), in lateral view with apex slightly enlarged (Fig. 43b).

Measurements and proportions.— Four samples studied, and data for two presented in tables 3 and 4.

Variation.— Specimens from central Europe, Ural Mountains in USSR and Tien-shan Mountains (USSR and China) do not differ significantly in means of measurements and proportions. However, specimens from Tien-shan Mountains seem smoother because the elytral pits are only slightly impressed, and because the lateral ridges of pits are indistinctly outlined. Thus, I assume there is gene flow or that gene flow was interrupted recently. However, the darker adults of the Italian sample differ significantly in the means of EL/HW and PW/HW and in their smaller size(EL, EW, PL and PW) from the above three samples. I feel that this mountain form is not connected by gene flow to the main French population, but my sample is too limited to confirm this. I have not seen specimens from the Balkan Mountains, but some of the character states in Obenberger's description (*in* Louvet, 1925) suggest that the Balkan specimens might represent a mountain race: pronotum and elytra more coarsely punctate; elytra shorter, elytral pits slightly impressed; dorsal body surface dark green or blue.

Distribution.— This Palaearctic species ranges from the Atlantic Coast (Scandinavia to central France) across Russia, northern Italy (Apennine Mountains) Bulgaria (Balkan

Table 4. Descriptive statistics for *E. uliginosus* based on four males and seven females from central Italian Apennine Mountains.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.0	1.99	0.071	0.027	2.4
PW	2.1–2.4	2.27	0.135	0.054	4.0
EL	4.5–5.1	4.74	0.276	0.111	3.9
EW	1.7–1.8	1.76	0.092	0.037	3.5
HW	2.2–2.4	2.29	0.102	0.041	3.0
B. Proportions					
PL/PW	0.844–0.920	0.873	0.038	0.015	2.9
PL/EL	0.402–0.445	0.419	0.018	0.007	2.8
PL/EW	1.070–1.190	1.130	0.050	0.020	3.0
PL/HW	0.840–0.910	0.867	0.030	0.012	2.3
PW/EL	0.465–0.495	0.480	0.014	0.006	2.0
PW/EW	1.250–1.340	1.300	0.045	0.018	2.3
PW/HW	0.966–1.020	0.994	0.031	0.012	2.0
EL/EW	2.620–2.790	2.700	0.078	0.031	1.9
EL/HW	2.000–2.150	2.070	0.067	0.027	2.1
EW/HW	0.723–0.807	0.768	0.034	0.014	3.0

Mountains), southern Russia (Caucasus), east to Western Siberia (Yenisey River), and westernmost China (Tien-shan Mountains). The report of this species from the Amur River (Louvet, 1925) requires confirmation. Kryzhanouskij (*in litt.*) observed a similar distribution. I have seen specimens from: France, Italy, Switzerland, Austria, Germany, Denmark, Sweden, Poland, USSR as far east as the Tien-shan Mountains.

Collecting notes.— Adults occur on wet, sandy loam with abundant mosses (*Amblystegium, Paludela,* rarely *Sphagnum*); small bullrushes (Juncaceae), sedges (*Carex* spp.) and *Myrica gale* (Lindroth, 1945) are also generally present.

Taxonomic notes.— The type series was not available for study, but S.G. Larson determined two specimens as *E. cupreus* and one as *E. uliginosus* (Zimsen, E., 1964). Larson (Zimsen, 1964) did not designate a lectotype. Since I did not see the specimens, I prefer not to designate a lectotype. However, Fabricius (1792,1801) describes adults as greenish-bronze. Thus, Fabricius was not referring to *E. cupreus,* but to *E. uliginosus* as understood traditionally. Schonherr did not describe *E. latithorax,* but Dejean saw the labelled specimen and used the name. Specimens of *E. bedeli* and *E. viridicupreus* probably represent the copper and brilliant green forms of the typical *E. uliginosus* in France. I have seen specimens of *E. uliginosus* from the Ural region and I assume that *E. impressifrons* is the same species. *E. italicus* probably refers to the Italian Appennine form, *E. uliginosus purkynei* refers to the Balkan population, and *E. uliginosus laevisculptus* refers to the populations inhabiting the mountains of Tien-shan in the western Himalaya. Xambeu (1898. 1901) described larvae supposedly of this species. However, his larvae cannot be assigned to *Elaphrus* (occipital suture lacking and nasale bidentate); moreover, the habitat described (streams) is most unlikely for

Table 5. Descriptive statistics for *E. pyrenaeus* based on 10 males and 10 females from the French and Spanish Pyrenees.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.1	2.00	0.118	0.035	3.9
PW	2.1–2.4	2.27	0.150	0.045	4.4
EL	4.2–5.1	4.71	0.320	0.095	4.5
EW	1.5–1.9	1.73	0.171	0.051	6.6
HW	2.0–2.3	2.18	0.124	0.037	3.8
B. Proportions					
PL/PW	0.856–0.930	0.879	0.032	0.010	2.4
PL/EL	0.404–0.456	0.425	0.020	0.006	3.2
PL/EW	1.060–1.330	1.150	0.084	0.025	4.9
PL/HW	0.878–0.964	0.916	0.031	0.009	2.3
PW/EL	0.450–0.511	0.484	0.023	0.007	3.2
PW/EW	1.220–1.430	1.310	0.078	0.023	3.9
PW/HW	1.000–1.080	1.040	0.035	0.011	2.3
EL/EW	2.530–3.000	2.710	0.158	0.047	3.9
EL/HW	2.070–2.240	2.160	0.079	0.023	2.4
EW/HW	0.723–0.828	0.796	0.040	0.012	3.3

this species.

I have seen 110 specimens, and dissected seven males.

Geographical affinities.— The range of this species overlaps with that of *E. cupreus*, a member of the *cupreus* group.

Elaphrus pyrenoeus Motschulsky
Figs. 44a-b, 120, 138

Elaphrus pyrenoeus Motschulsky, 1850b:LXVI. Type locality: Pryénées; type not seen.
Elaphrus uliginosus var. pyrenoeus; Laboulbène, 1850:LXVII.
Elaphrus splendidus; Gaubil, 1849:14 (*nec* Fischer von Waldheim, 1828).
Elaphrus uliginosus var. *pyrenaeus;* Fairmaire and Laboulbène, 1854:7. Fauvel, 1882:82. Marseul, 1882:4. Seidlitz, 1891:19. Semenov, 1895:312. Jacobson, 1906:267. Obenberger, 1917:9. Bänninger, 1919:147. Louvet, 1925:20. Jeannel, 1941:218. Invalid emendation.
Elaphrus pyrenaeus; Jeanne, 1966:16.
Elaphrus pyrenaeus nevadensis Jeanne, 1966:18. Type locality: Puerto de la Ragua, Sierra Nevada, Granada, 1850 m.; type in Jeanne's collection, Bordeaux France; type seen by me. NEW SYNONYM.

Adults

Diagnostic combination.— Distinguished from adults of *E. fuliginosus* by brilliant metallic green or brown copper dorsal body surface, by lack or presence of suggested meshes of microsculpture on intervals 4, 6 and 8, and by deeply impressed elytral pits (Fig. 120).

Description.— Upper body surface brilliant metallic green or in few specimens brilliant brown copper; ventral surface metallic golden green; most surfaces of legs and palpi dark blue.

Pronotum relatively long: means of PL/PW and PL/HW significantly higher than those of samples of *E. uliginosus*. Elytral pits deeply impressed (Fig. 120), lateral ridges narrowly outlined or absent, and intervals 4, 6 and 8 not costate.

Integument sculpture. Punctures similar in distribution to that of *E. uliginosus* but finer dorsally and denser ventrally (most adjacent punctures in contact on proepisternum).

Meshes of microsculpture restricted: present near elytral shoulder, otherwise absent from or indistinctly outlined on intervals 4, 6 and 8 (Fig. 138).

Male genitalia. Apex of median lobe similar to that of males of *E. uliginosus,* but in dorsal view apex more twisted (Fig. 44).

Measurements and proportions.— Two samples studied, and one presented in Table 5.

Variation.— I found little noteworthy variation between the samples from the Pyrénées and the Sierra Nevada, but the latter sample consisted of only two specimens. Thus, until further material is obtained, I prefer not to recognize *E. pyrenoeus nevadensis.*

Distribution.— I have seen specimens from the French and Spanish Pyrénées and also the type from the Sierra Nevada. Jeanne (1966) reported them from the following Spanish provinces: Lérida, Huesca, Basses Pyrénées, Navarra, Leon, Oviedo and Segovia. Louvet (1925) reported them from the Alps and Beaujolais Mountains, but I have not seen these specimens.

Collecting notes.— Found in subalpine and alpine mossy bogs (Jeanne, 1966).

Taxonomic notes.— I have seen 32 specimens and dissected three males.

Geographic affinities.— This species is allopatric in relation to all other known member of *Neoelaphrus.*

Elaphrus potanini Semenov

Elaphrus potanini Semenov, 1889:352. Type locality: China, Gan-ssu (Kansu in current spelling) at Amdo; type not seen. Jacobson, 1906:267.

Adults

Diagnostic combination.— Distinguished from adults of other species of subgenus by brilliant brown color of dorsal body surface, and by metallic green elytral pits.

Description.— Dorsal body surface brown with copper luster; elytral pits, postero-lateral angles of pronotum, and anterior portion of head metallic green; antennomeres 1 to 3, femur (except base), base of tibia, and dorsal surface of tarsomeres metallic golden-green; base of femur and middle of tibia dark reddish brown; palpi brown.

Pronotum transverse and wider than head; lateral margin deeply sinuate; postero-lateral angles rather prominent and acute; anterior transverse stria deeply impressed near middle; main discal impression slightly impressed; medial stria deep and short. Elytra elongate, pits well impressed, lateral ridges obsolete; mirrors not sharply outlined in intervals 3 and 5.

Integument sculpture. Punctures fine and dense over most of dorsal body surface. Microsculpture undescribed.

Male genitalia. Undescribed.

Distribution.— The type specimen is from the Chinese province fo Kansu at Amdo, collected on May 22, 1885.

Taxonomic notes.— This species is known to me only through Semenov's description. I included it in this group because of the deeply impressed anterior transverse stria of the pronotum, and also the transverse pronotum that is wider than the head. I believe that it represents a distinct species because of its unusual coloration, and its short and transverse pronotum. Based on previous experience with Semenov's species, I trust his judgement.

Besides the type, Kryzhanoskij (*in litt.*) reported three additional specimens.

Geographical affinities.— Probably allopatric in relation to all other known members of *Neoelaphrus.*

THE *FULIGINOSUS* GROUP

Adults

Diagnostic combination.— Fringe of setae on posterior margin of pronotum ending 150 to 200 microns from postero-lateral angles (Fig. 18a); lateral margin of pronotum, in lateral view, not depressed near middle, pronotal epipleuron not narrowest at middle (shaped as in Fig. 18b); bead of lateral margin of pronotum 20 to 30 microns in width, or lacking. Tibia of foreleg of male with one small projection at base of apical spur and one large projection at base of posterior spur--best seen in posterior view (Fig. 149). Punctures of proepisternum 30 to 45 microns in diameter, area near punctures widely depressed (diameter of depression about 80 microns)--best seen on proepisternum (Fig. 107).

All Instar Larvae

Diagnostic combination.— All instars: epicranial suture subequal to inner edge of antennomere 1; pointed microsculpture lacking or slightly developed baso-laterally.

Second and third instar larvae: parietale mostly pale except near frontale suture, and without pointed microsculpture dorso-laterally; urogomphus with nine or more accessory setae.

The three species of this group are restricted to the temperate Nearctic region.

Elaphrus fuliginosus Say

Figs. 18a-b, 45a-b, 158

Elaphrus fuliginosus Say, 1834:417. Type locality: originally Pennsylvania, but Lindroth and Freitag (1969) designated a male neotype from Rumney, New Hampshire; neotype in Museum of Comparative Zoology, Massachusetts; neotype seen by me. Crotch, 1873:4. 1876:246; Schaupp, 1878:6. Blatchtley 1910:48. Lindroth, 1961:114.
Elaphrus clairvillei; LeConte, 1848:448 (*nec* Kirby, 1837). Crotch, 1873:4. 1876:246. Schaupp, 1878:6.

Adults

Diagnostic combination.— Distinguished from adults of *E. cicatricosus* and *E. lindrothi* by well developed and wide (20 to 30 microns) bead on lateral margin of pronotum, and by dark metallic green color of dorsal surface. Specimens of *E. fuliginosus* are likely to be confused with some members of the *uliginosus* group (especially with specimens of *E. uliginosus*). Distinguished from *E. uliginosus,* by green tibiae and tarsomeres.

Description.— Dorsal body surface dark green except for purple pits; ventral body surface dark golden-green, but abdomen piceous; legs and palpi brown or reddish-brown with a metallic green hue.

Lateral margin of pronotum completely beaded; pronotum with sharply impressed median longitudinal and anterior transverse striae; disc with two pairs of weakly suggested impressions antero-laterally. Mirrors of elytral intervals 3 and 5 sharply outlined, and markedly contrasted against microsculptured, green, and densely punctate intervals 4 and 6. Elytral pits moderately impressed, with narrow lateral ridges and with 20 to 25 punctures. Abdominal sternum 7 of males with numerous accessory setae, and of females with fewer than four.

Trochanter of foreleg with two setae. Femur of foreleg, midleg and hindleg with about 60, 60, and 10 setae respectively. Tibia of foreleg, midleg and hindleg with about 25, 80, and 80 setae respectively.

Integument sculpture. Punctures 20 to 30 microns in diameter on coxae and scutellum, 30 to 40 microns in diameter on clypeus, on head, on pronotum and elytral intervals, and 40 to 45 microns in diameter on pleura and sterna. Punctures 20 to 80 microns apart on dorsal body surface, and on average 40 microns apart on thoracic sterna and pleura, 40 to 120 microns apart laterally on abdominal sterna.

Microsculpture flat on dorsal surface except on mirrors, and convex in elytral pits and near postero-lateral angles of pronotum.

Male genitalia. Apex of median lobe in dorsal view thin-edged (Fig. 45a), and in lateral view with angular projection ventrally (Fig. 45b).

Measurements and proportions.— Two samples studied, and data for one presented in Table 6.

Table 6. Descriptive statistics for *E. fuliginosus* based on 10 males and 10 females from Brooklyn, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.0–2.4	2.23	0.188	0.097	4.7
PW	2.2–2.6	2.45	0.143	0.043	3.9
EL	4.5–5.4	5.00	0.349	0.104	4.6
EW	1.5–2.0	1.84	0.139	0.041	5.0
HW	2.3–2.7	2.51	0.156	0.047	4.1
B. Proportions					
PL/PW	0.875–0.942	0.915	0.023	0.007	1.6
PL/EL	0.426–0.458	0.442	0.014	0.004	2.1
PL/EW	1.170–1.260	1.210	0.039	0.012	2.1
PL/HW	0.840–0.916	0.891	0.031	0.009	2.3
PW/EL	0.462–0.495	0.483	0.014	0.004	1.9
PW/EW	1.280–1.390	1.320	0.040	0.012	2.0
PW/HW	0.941–1.000	0.974	0.026	0.008	1.8
EL/EW	2.670–2.810	2.740	0.061	0.018	1.5
EL/HW	1.960–2.080	2.020	0.051	0.015	1.7
EW/HW	0.713–0.772	0.735	0.024	0.007	2.2

Variation.— I found no significant differences between two distant samples: one from Manitoba and Minnesota, and one from Brooklyn, New York. Specimens of the western sample were slightly larger on average.

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species of the group as follows: nasale toothed; pointed sculpture present near suture of mesonotum and metanotum.

First Instar Larvae

Description.— Dorsal surface of parietale pale except anteriorly near antennae, along frontale and occipital sutures. Nasale toothed. Pointed sculpture of parietale restricted baso-laterally (5% of dorsal surface). Meshes of microsculpture present on 15% of each sclerite of mesonotum and metanotum; pointed sculpture present near suture of both nota.

Second Instar Larvae

Description.— Pronotal epipleuron with one or two accessory setae; pronotum with meshed microsculpture on 10% of surface. Mesonotal epipleuron with one accessory seta; meshed microsculpture present on 40% of mesonotum, pointed microsculpture restricted to lateral portion (10% of surface). Metathorax as mesothorax. Each sclerite of terga 1 to 8 with about 25 accessory setae, and urogomphus with nine (Fig. 98b). Pointed microsculpture restricted on tergum 1, widespread on terga 2 to 8, clearly outlined and shaped as small scales on urogomphus, and multipointed on tergum 10. Pointed microsculpture restricted to lateral portion of posterior bank of terga 1 to 8 (5% of surface), and of anterior band of tergum 9 (10% of surface). Epipleuron and hypopleuron of terga 2 to 8 each with about eight accessory setae. Sternite of abdominal segment 8 with about 15 accessory setae.

Third Instar Larvae

Description.— Each sclerite of pronotum with about 20 accessory setae; meshes of microsculpture absent from disc. Each sclerite of mesonotum with about 85 accessory setae. Mesosternite without accessory setae. Largest projection of urogomphus in lateral view large (Fig. 98c); each sclerite of terga 1 to 8 with about 70 accessory setae, and urogomphus with nine; pointed microsculpture on 5% of anterior band of terga 1 to 8, and on 20% of anterior band of tergum 9; microsculpture barely suggested on urogomphus. Epipleuron of segments 2 to 8 with about 30 accessory setae. Hypopleuron of segments 1 to 8 with about 25 accessory setae. Outer poststernite of segment 1 with about eight accessory setae, and of segments 2 to 7 with about 14. Inner poststernite of segment 1 with two accessory setae, and of segments 2 to 7 each with four.

Geographical Distribution and Affinities, and Notes

Distribution.— From the Atlantic coast of Maine to Maryland, west to Manitoba and Nebraska (Fig. 158).

Collecting notes.— According to Larochelle (1975) adults are found in open places with sparse vegetation on wet sandy soil. I found two specimens in a similar habitat.

Taxonomic notes.— I examined 275 adults, and dissected five males. I studied three first instar, one second instar, and one third instar larvae from Vermont.

Geographical affinities.— The range of this species overlaps with that of all species of the *uliginosus* group at least in Maryland, and with those of *E. clairvillei* and *E. olivaceus* in the northern half of its range.

Elaphrus cicatricosus LeConte

Figs. 47a-b, 99a-b, 107, 139, 145, 146, 147, 148, 149, 150, 159

Elaphrus cicatricosus LeConte 1848:448. Type locality: Central New York State; type in Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts; type seen by me. LeConte 1853:402. Crotch, 1873:4. 1876:246. Schaupp: 1878:6. Lindroth, 1961:114.

Elaphrus rhodeanus Casey, 1924:17. Type locality: Boston Neck, Rhode Island; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington D.C. Lindroth, 1961:114.

Adults

Diagnostic combination.— Distinguished from adults of other species of the group by unbeaded lateral margin of pronotum and by large lateral ridges in pits of elytra.

Description.— Dorsal body surface dark brown with copper luster except for purple pits; ventral surface black but abdominal sterna dark piceous; legs brown with green metallic hue on femur and blue metallic hue on tibia and tarsomeres. Lateral margin of pronotum unbeaded; pronotum with sharply impressed medial stria and indistinctly outlined anterior transverse stria; disc without antero-lateral impression. Mirrors of elytral intervals 3 and 5 sharply outlined, but little contrasted against dark and sparsely punctate intervals 4 and 6. Elytral pits deeply impressed, with large and convex lateral ridges, and with four to eight punctures. Abdominal sternum 7 of males and females without or with one or two accessory setae.

Trochanter of foreleg with one seta. Femur of foreleg, midleg and hindleg with about 30, 30 and six setae respectively. Tibia of foreleg, midleg and hindleg with about 20, 55 and 55 setae respectively.

Integument sculpture. Punctures 20 to 30 microns in diameter on coxae, 30 to 40 microns in diameter on dorsal body surface, and 40 to 45 microns in diameter on ventral body surface. Punctures 10 to 200 microns apart on dorsal body surface, 10 to 90 microns apart on pleura, and 70 to 150 microns apart on sterna.

Microsculpture subconvex on dorsal body surface, convex in elytral pits, and near postero-lateral impression of pronotum, and flat on ventral body surface.

Male genitalia. Apex of median lobe in dorsal view thick-edged (Fig. 47a), and in lateral view with round and weak ventral projection (Fig. 47b).

Measurements and proportions.— Two samples studied, and data for one presented in Table 7.

Table 7. Descriptive statistics for *E. cicatricosus* based on 10 males and 10 females from Maclean Bog, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.0–2.3	2.11	0.116	0.035	3.7
PW	2.2–2.5	2.32	0.135	0.040	3.9
EL	4.5–5.2	4.86	0.270	0.080	3.7
EW	1.6–1.9	1.79	0.129	0.038	4.8
HW	2.3–2.6	2.44	0.106	0.032	2.9
B. Proportions					
PL/PW	0.872–0.966	0.909	0.033	0.010	2.4
PL/EL	0.422–0.454	0.435	0.019	0.005	2.4
PL/EW	1.130–1.240	1.190	0.050	0.015	2.8
PL/HW	0.828–0.911	0.865	0.026	0.008	2.0
PW/EL	0.454–0.510	0.479	0.020	0.006	2.7
PW/EW	1.250–1.370	1.310	0.061	0.018	3.1
PW/HW	0.907–0.990	0.952	0.030	0.009	2.1
EL/EW	2.620–2.840	2.740	0.099	0.029	2.4
EL/HW	1.900–2.060	1.990	0.065	0.019	2.2
EW/HW	0.697–0.767	0.726	0.032	0.009	2.9

Variation.— I found no significant differences between means of samples from northern New York and New Jersey.

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species of the group by lack of teeth on nasale, and of microsculpture near suture of mesonotum and metanotum.

First Instar Larvae

Description.— Dorsal surface of parietale pale except anteriorly near antennae and along suture of frontale. Nasale not toothed. Pointed microsculpture absent from parietale. Meshes of microsculpture present on 10 to 12% of each sclerite of mesonotum and metanotum; pointed microsculpture lacking on both nota.

Second Instar Larvae

Description.— Pronotal epipleuron with seven accessory setae; pronotum without microsculpture. Mesonotal epipleuron with five accessory setae; mesonotum without microsculpture. Metathorax as mesothorax. Each sclerite of terga 1 to 8 with 36 accessory setae, and urogomphus with 25 (Fig. 99a). Pointed microsculpture of terga 1 to 8 restricted (5% of surface), indistinct on urogomphus, and single-pointed on tergum 10. Pointed microsculpture absent from posterior band of terga 1 to 8, and from anterior band of tergum 9. Epipleuron and hypopleuron of segments 1 to 8 each with about 25 accessory setae. Sternite of abdominal segment 8 with about 22 accessory setae.

Third Instar Larvae

Description.— Each sclerite of pronotum with about 40 accessory setae; meshes of microsculpture absent from disc. Each sclerite of mesonotum with more than 100 accessory setae. Mesosternite with three accessory setae. Largest projection of urogomphus medium-sized in lateral view. (Fig. 99b); terga 1 to 8 each with about 140 accessory setae, and

urogomphus with about 30; pointed microsculpture absent from anterior band of terga 1 to 9; microsculpture absent from urogomphus. Epipleuron of segments 2 to 8 with 40 to 60 accessory setae. Hypopleuron of segments 1 to 8 with 25 to 50 accessory setae. Outer poststernite of segment 1 with about 15 accessory setae, and of segments 2 to 7 with about 18. Inner poststernite of segment 1 with five accessory setae, and of segments 2 to 7 each with seven.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends in the north from Michigan, southern Quebec and Maine, south to Tennessee and Maryland (Fig. 159).

Collecting notes.— I found these beetles in various localities on wet, relatively firm organic mud near slow-flowing brooks where alders grew commonly, usually in the shade of larger trees. These observations match well with those of Lindroth, Darlington (Lindroth, 1961:114), Frost (1910) and Masner (pers. comm.).

Taxonomic notes.— The type of *E. rhodeanus* matches typical specimens of *E. cicatricosus.*

I examined 250 adults and dissected four males. I studied three first instar, three second instar, and three third instar larvae from Maclean Bog, New York.

Geographical affinities.— The ranges of *E. fuliginosus* and this species nearly completely overlap. At the southeastern end of its range, this species is sympatric with *E. lindrothi.* In the northern half of its range, *E. cicatricosus* overlaps with those of *E. clairvillei* and *E. olivaceus.*

Elaphrus lindrothi new species
Figs. 46a-b, 104, 121, 159

Elaphrus lindrothi new species. Type material: holotype male and allotype female labelled "Ill., Jackson Co., 3 mi. n. Pomona -- 37° 41′ N 87° 20′ W, 1, V, 79, H. Goulet"; type (No. 18010) in Canadian National Collection, Ottawa. Additional paratypes deposited in collections of CNCI, MCZC, USNM, UASM and CASC.
Elaphrus cicatricosus; Blatchley, 1910:49 (*nec* LeConte, 1848).

Adults

Diagnostic combination.— Distinguished from adults of other species of group by unbeaded lateral margin of pronotum, and by barely suggested lateral ridges of the elytral pits.

Description.— Dorsal body surface dark silver; ventral body surface black or dark brown, but abdominal sterna brown; legs, palpi and antennomeres 1 to 3 reddish brown; femora, tibiae and tarsomeres with metallic purple hue.

Lateral margin of pronotum unbeaded; pronotum with weakly impressed medial longitudinal stria, and with sharply impressed anterior transverse stria; disc without antero-lateral impression. Mirrors of interval 3 weakly outlined, and contrasted against silver, and densely punctate intervals 2 and 4. Pits of elytra impressed, without or with barely suggested lateral ridges (Fig. 104), and with about 10 to 15 punctures. Abdominal sternum 7 of males and females without accessory setae.

Trochanter of foreleg with two setae. Femur of foreleg, midleg and hind leg with about 30, 30 and five setae respectively. Tibia of foreleg, midleg and hindleg with about 20, 55 and 55 setae respectively.

Integument sculpture. Punctures 20 to 25 microns in diameter on coxae, clypeus, head, pronotum and on elytral intervals, and 30 to 35 microns in diameter on pleura and sterna. Punctures 10 to 30 microns apart on head and on elytral intervals 4, 6 and 8 (Fig. 121), 20 to 40 microns apart on pronotum (Fig. 104), and 20 to 90 microns apart on ventral body surface.

Microsculpture subconvex on dorsal body surface, on pleura of prothorax and mesothorax, and flat on remaining ventral body surface.

Male genitalia. Apex of median lobe in dorsal view thin-edged (Fig. 46a), and in lateral view with angular ventral projection (Fig. 46b).

Measurements and proportions.— One sample studied. See Table 8.

Variation.— Except for those from Illinois, samples were too small for analysis. Samples on eastern and western extremes of the geographical range appear similar.

Table 8. Descriptive statistics for *E. lindrothi* new species based on three males and five females from southern Indiana and Maryland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.83	0.132	0.062	4.8
PW	1.7–2.1	1.87	0.195	0.092	6.6
EL	3.8–4.4	4.15	0.346	0.163	5.6
EW	1.5–1.7	1.61	0.148	0.070	6.1
HW	2.0–2.3	2.18	0.136	0.064	4.2
B. Proportions					
PL/PW	0.878–0.973	0.929	0.052	0.025	3.7
PL/EL	0.415–0.477	0.440	0.029	0.014	4.4
PL/EW	1.060–1.220	1.130	0.079	0.037	4.7
PL/HW	0.820–0.851	0.839	0.016	0.008	1.3
PW/EL	0.441–0.503	0.475	0.030	0.014	4.2
PW/EW	1.170–1.290	1.220	0.072	0.034	3.9
PW/HW	0.852–0.953	0.905	0.051	0.024	3.8
EL/EW	2.490–2.680	2.570	0.093	0.044	2.4
EL/HW	1.780–1.980	1.910	0.100	0.047	3.5
EW/HW	0.698–0.779	0.742	0.042	0.020	3.8

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species of the group by lack of teeth on nasale, and by presence of pointed microsculpture near suture of mesonotum and metanotum.

First Instar Larvae

Description.— Parietale mostly dark except behind eyes. Nasale without teeth. Pointed microsculpture of parietale restricted baso-laterally (5 to 10% of dorsal surface). Meshes of microsculpture present over 50% of surface of mesonotum and metanotum; pointed microsculpture present along suture of both nota as wide bands (25% of surface).

Second Instar Larvae

Description.— Parietale dark near frontale and epicranial suture only. Pronotal epipleuron with two or three accessory setae; pronotum with meshes of microsculpture over surface. Mesonotal epipleuron with one or two accessory setae; meshed microsculpture present over most of mesonotum, and pointed microsculpture present laterally (10% of disc surface) and near suture (10% to 20% of disc surface). Each sclerite of terga 1 to 8 with about 25 accessory setae, and urogomphus with nine to 14. Pointed microsculpture developed on all of terga 1 to 8 and urogomphus, and single-pointed on tergum 10. Pointed microsculpture absent form posterior bands of terga 1 to 8, and present on anterior band of tergum 9 (5% of surface). Epipleuron and hypopleuron of segments 2 to 8 each with about 15 accessory setae. Sternite of segment 8 with 12 to 15 accessory setae.

Third Instar Larvae

Description.— Each sclerite of pronotum with about 40 accessory setae; meshes of microsculpture widespread but weakly outlined. Each sclerite of mesonotum and metanotum with more than 100 accessory setae. Mesosternite with two to three accessory setae. Largest projection of urogomphus in lateral view large (Fig. 98c); each sclerite of terga 1 to 8 with about 110 accessory setae, and urogomphus with nine to 14; pointed microsculpture absent from anterior band of terga 1 to

8, and present on anterior band of tergum 9 (5% of surface); microsculpture absent from urogomphus. Epipleuron of segments 2 to 8 with 40 to 60 accessory setae. Hypopleuron of segments 1 to 8 with 25 to 50 accessory setae. Outer poststernite of segment 1 with eight to 13 accessory setae, and of segments 2 to 7 with 18 to 20. Inner poststernite of segments 2 to 7 with three to six accessory setae.

Geographical Distribution and Affinities, and Notes

Derivation of specific epithet.— I name this species in honor of the late Prof. C.H. Lindroth, who contributed immensely to a better understanding of North American carabids, and provided a solid base for further study of the Elaphrini.

Distribution.— Known from eastern United States (Fig. 159). Localities are listed below.

United States. MARYLAND: Priest Bridge (1;USNM), Bowie (2:USNM). INDIANA: Knox County (4;PURC), Hovey Lake (1;PURC). ILLINOIS: Union County (3;CNCI), Jackson County, 3 mi. n. Pomona (70; CASC, CNCI, MCZC, USNM, UASM).

Collection notes.— In Illinois, many adults were found in the shade of bald cypresses on clay flats, covered partly with rotted leaves. In springtime, before the cypresses are fully leafed, numerous *E. ruscarius* were found also in this habitat. This habitat is similar to those observed by Blatchley (1910) in southern Indiana for his "*E. cicatricosus*".

Taxonomic notes.— I examined 81 adults, and dissected four males. I studied seven first instar, three second instar, and three third instar larvae from Pomona, Illinois.

Geographical affinities.— The range of this species overlaps with those of *E. fuliginosus* and *E. cicatricosus.*

THE *CUPREUS* GROUP

Adults

Diagnostic combination.— Fringe of setae on posterior margin of pronotum ending near postero-lateral impressions (200 microns or more from postero-lateral angles) (Fig. 19); lateral margin of pronotum, in lateral view, not depressed near middle, pronotal epipleuron not narrowest at middle (shaped as in Fig. 18b); bead of lateral margin of pronotum 10 to 15 microns in width. Tibia of foreleg of males without projection at base of apical and posterior spur. Punctures of proepisternum 25 to 30 microns in diameter, and surrounding surface narrowly impressed or not.

Larvae

Diagnostic combination.— All instars: epicranial suture subequal or longer than outer edge of antennomere 1; pointed microsculpture present baso-laterally on 5% or more of parietale dorsal surface.

Second and third instar larvae: parietale mostly dark except behind eye and/or base, and with pointed microsculpture dorso-laterally (15% or more of surface); urogomphus with seven accessory setae.

The five species of this group occur in temperate and boreal regions of the northern hemisphere.

Elaphrus sibiricus Motschulsky
Fig. 48a-b

Elaphrus sibiricus Motschulsky, 1846:71. Type locality: probably Irtysh River, USSR, type not seen. Solsky 1872:232, 233. Marseul, 1880:66. Bates, 1883:205, 217. Jacobson, 1906:267. Nakane, 1955:22. 1963:18.

Elaphrus dauricus Morawitz, 1863:191. Type locality: probably Dauria (region s.e. of Lake Baikal), USSR; type not seen. Solsky, 1872: 232, 233. Marseul, 1880:29. Jacobson, 1906:267.

Table 9. Descriptive statistics for *E. sibiricus* based on nine males and five females from eastern Siberia, northeastern China and northern Japan.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.1	1.98	0.150	0.053	5.0
PW	2.1–2.4	2.28	0.157	0.055	4.6
EL	4.5–5.2	4.89	0.256	0.091	3.5
EW	1.6–1.8	1.74	0.105	0.035	4.0
HW	2.1–2.4	2.27	0.120	0.043	3.5
B. Proportions					
PL/PW	0.805–0.910	0.869	0.045	0.016	3.5
PL/EL	0.385–0.421	0.404	0.015	0.005	2.5
PL/EW	1.060–1.180	1.130	0.054	0.019	3.2
PL/HW	0.841–0.899	0.871	0.029	0.010	2.2
PW/EL	0.437–0.480	0.466	0.017	0.006	2.5
PW/EW	1.260–1.330	1.300	0.034	0.012	1.7
PW/HW	0.943–1.050	1.000	0.047	0.017	3.1
EL/EW	2.740–2.880	2.800	0.072	0.028	1.7
EL/HW	2.090–2.220	2.150	0.056	0.020	1.7
EW/HW	0.742–0.811	0.769	0.031	0.011	2.7

Elaphrus cupreus; Solsky, 1872:233 (*nec* Duftschmid, 1812).

Adults

Diagnostic combination.— Distinguished from adults of other species of the group by green tarsomeres; and by well developed meshes of microsculpture on elytral intervals 4, 6 and 8.

Description.— Upper body surface brilliant green in impressions, dark green or bronze-green elsewhere except for purple pits; ventral body surface dark golden-green to nearly black medially; legs and palpi piceous except for metallic green reflection on femora, apex of tibiae, and tarsomeres.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with two pairs of submedial impressions. Prosternal process with one to six accessory setae. Metasternum with few punctures medially; all punctures setose. Abdominal sterna 5 and 6 each with five to 10 accessory setae, sternum 7 in males with 10 to 20, and in females with 10 or less. Setigerous punctures of elytron distinctly outlined. Elytral pits well impressed, and with 10 to 15 punctures; lateral ridges of pits wide, and not fused anteriorly and posteriorly (Fig. 132). Mirrors sharply outlined and contrasted on intervals 3, or 3 and 5. Number of setae on legs not studied in detail, but similar to those of adults of *E. clairvillei*. Tibia of midleg of males with sharp apical projection at base of inner spur (Fig. 150). Hind coxa with punctures on outer half, and with eight to 15 accessory setae on inner half.

Integument sculpture. Punctures 25 to 35 microns in diameter on clypeus, head, pronotum and on elytral intervals 4, 6 and 8, 30 to 35 microns in diameter on pleura and laterally on thoracic and abdominal sterna. Punctures 30 to 50 microns apart on clypeus, head, lateral portions of pronotum, elytral intervals 4, 6 and 8, on pleura, and on lateral portions of thoracic and abdominal sterna.

Microsculpture on head, pronotum, elytral intervals 4, 6 and 8, pleura, and thoracic and abdominal sterna subconvex or convex.

Male genitalia. Apex of median lobe in lateral view wide and angular ventro-apically (Fig. 48b); in dorsal view, apex straight, thick-edged (40 microns), and extended far posteriorly from apex of internal sac (Fig. 48a).

Measurements and proportions.— One sample studied. See Table 9.

Variation.— I could not study this aspect as I had too few specimens.

Distribution.— The range of this species extends from central eastern Siberia and Mongolia, to northeastern China, northern Japan and Kamchatka. I have seen specimens from the following localities: USSR: Lake Baikal (BMNH, MCZ, UASM), Tschita (MCZ), Amur River (BMNH), and Ussuri River (MCZ); CHINA: Hailar (MCZ); JAPAN: Rebun Island. Kryzhanovskij (*in litt.*) reported adults from as far west as Krasnoyarsk and Yakutsk region (Jakutia) and from Kamchatka in the northeast.

Collecting notes.— One specimen was found on a stream bank (Ball pers. comm.). I have seen a slightly tanned male collected in mid-August. Thus adults probably overwinter.

Taxonomic notes.— According to the descriptions, adults of *E. dauricus* match those of *E. sibiricus*.

I studied nine males and five females, and dissected three males.

Geographical affinities.— Found sympatrically with *E. cupreus,* a member of the *cupreus* group, and with *E. splendidus* and *E. japonicus*, both members of the *uliginosus* group.

Elaphrus cupreus Duftschmid

Figs. 19, 49a-b, 108, 132

Elaphrus cupreus Duftschmid, 1812:194. Type locality: probably Germany; type not seen. Dejean, 1826:271. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Schiødte, 1841:356. Chaudoir, 1842:815. Küster, 1846:7. Letzner, 1849:50. Fairmaire and Laboulbène, 1845:6. Schaum, 1860:68. Stierlin, 1869:11. Redtenbacher, 1874:6. Seidlitz, 1875:2. Sahlberg, 1880:10. Bedel, 1881:23. Fauvel, 1882:81, 83. Marseul, 1882:4. Redtenbacher, 1874:6. Seidlitz, 1891:19. Ganglbauer, 1892:123. Everts, 1898:49. Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhnt, 1912:50. Fairmaire, 1913;31. Schaufuss, 1916:29. Bänninger, 1919:148. Porta, 1923:78. Portevin, 1929:41. Jacobson, 1931:81. Joy, 1932:328. Jeannel, 1941:218. Lindroth, 1974:33.

Elaphrus riparius; Olivier, 1790:4 (*nec* Linnaeus, 1758). Dejean, 1826:271. Schaum, 1856:68. Marseul, 1882:4. Ganglbauer, 1892:123. Semenov, 1895:313. Jacobson, 1906:267. Jeannel, 1941:218.

Elaphrus uliginosus; Illiger 1798:225 (*nec* Fabricius, 1792). Dejean, 1826:271. Schaum, 1856:68. Ganglbauer, 1892:123. Semenov, 1895:313. Jacobson, 1906:267. Jeannel, 1941:218.

Elaphrus arcticus; Dejean, 1826:272. Type locality: Lapland; type not seen. Fauvel, 1882:83. Semenov, 1895:313. Bänninger, 1919:148.

Elaphrus borealis Andersch (NOMEN NUDUM). Gaubil, 1849:14. Motschulsky, 1850a:5. Semenov, 1895:313.

Elaphrus cupreus var. *arcticus;* Marseul, 1882:4. Jacobson, 1906: 267.

Elaphrus cupreus var. *dauricus*; Marseul, 1882:4 (*nec* Morawitz, 1863).

Adults

Diagnostic combination.— Distinguished from adults of other species of this group by dark brown copper color of the dorsal surface of body, by purple tibiae and tarsomeres and by well outlined meshes of microsculpture on head, pronotum and intervals 4, 6 and 8 (Fig. 132).

Description.— Upper body surface dark brown with copper luster except for purple pits; ventral body surface dark golden green; legs and palpi piceus except for dark green hue on femora, and purple on apex of tibiae and tarsomeres.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with two pairs of submedial impressions. Prosternal process with one to four accessory setae. Metasternum with few punctures antero-medially; most punctures setose. Abdominal sterna 5 and 6 each with five to 15 accessory setae, sternum 7 in males with about 20 and in females with five to 10. Setigerous punctures of elytron distinctly outlined. Pits of elytron deeply impressed, and with 10 to 25 punctures; lateral ridges wide and not fused anteriorly and posteriorly (Fig. 132). Mirrors sharply outlined and contrasted on intervals 3, or 3 and 5. Number of setae on legs not studied in detail, but similar to those of adults of *E. clairvillei*. Tibia of midleg of males with sharp apical projection at base of inner spur (Fig. 150). Hind coxae with few punctures on outer 0.5, and with three to five accessory setae near inner margin.

Integument sculpture. Punctures 15 to 25 microns in diameter on clypeus, head, pronotum and on elytral intervals 4, 6 and 8, 30 microns in diameter on pleura and lateral portions of thoracic and abdominal sterna. Punctures 50 to 150 microns apart on head, on lateral portion of pronotum, and on elytral intervals 4, 6 and 8, 30 to 50 microns apart on pleura, and lateral portion of thoracic and abdominal sterna.

Table 10. Descriptive statistics for *E. cupreus* based on 10 males and 10 females from southern Sweden–Skane: Lomma Silvakra. (USNM)

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.93	0.119	0.035	4.1
PW	1.9–2.4	2.10	0.140	0.042	4.4
EL	4.5–5.0	4.81	0.213	0.063	3.0
EW	1.6–1.8	1.76	0.111	0.033	4.2
HW	2.1–2.3	2.22	0.097	0.029	2.9
B. Proportions					
PL/PW	0.843–1.010	0.922	0.054	0.016	3.9
PL/EL	0.383–0.430	0.402	0.018	0.005	3.0
PL/EW	1.030–1.250	1.100	0.077	0.023	4.7
PL/HW	0.814–0.910	0.869	0.040	0.012	3.0
PW/EL	0.408–0.461	0.436	0.020	0.006	3.1
PW/EW	1.130–1.330	1.190	0.065	0.019	3.6
PW/HW	0.893–0.978	0.943	0.039	0.012	2.8
EL/EW	2.650–2.910	2.730	0.094	0.028	2.3
EL/HW	2.070–2.270	2.160	0.065	0.019	2.0
EW/HW	0.711–0.831	0.793	0.040	0.012	3.3

Microsculpture on head, pronotum, elytral intervals 4, 6 and 8, pleura, and thoracic and abdominal sterna subconvex or convex.

Male genitalia. Apex of median lobe in lateral view wide and subangular ventro-apically (Fig. 49b); in dorsal view, apex straight, thick-edged (40 microns) and extended far posteriorly from apex of internal sac (Fig. 49a).

Measurements and proportions.— Six samples studied, and data for two presented in Tables 10 and 11.

Variation.— Specimens from southern Sweden resemble closely those from France, Germany and western Russia (Kaluga near Moscow). Four specimens from arctic Scandinavia are smaller than average. A single specimen east of the Caspian Sea seems typical, though darker. Three specimens from northeastern China differ slightly from European ones. Analysis of ratios suggests the same pattern. Samples of specimens from southern Sweden, Germany and western Russia are similar. Samples from southern Sweden and France are significantly different in the following means: PL/HW, EL/EW and EL/HW. However, the French sample is similar to those from Germany and Russia. Thus gene flow probably exists among these populations. The small sample from arctic Scandinavia consists of small specimens. The sample from northeastern China consists of small specimens with a high ratio PL/EL (0.410). Therefore, I think that gene flow exists between all European populations, and that the slightly modified northeastern Chinese sample may be connected by gene flow with the western Palaearctic samples.

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species of the group by restricted meshes of microsculpture on parietale (7% of dorsal surface).

Table 11. Descriptive statistics for *E. cupreus* based on 10 males and 10 females from Marne Region, France.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.0	1.91	0.100	0.030	3.4
PW	2.0–2.2	2.12	0.108	0.032	3.4
EL	4.6–5.1	4.78	0.192	0.059	2.7
EW	1.7–1.9	1.79	0.108	0.032	4.0
HW	2.2–2.4	2.26	0.077	0.023	2.3
B. Proportions					
PL/PW	0.849–0.964	0.904	0.041	0.012	3.0
PL/EL	0.376–0.430	0.400	0.022	0.006	3.6
PL/EW	0.948–1.160	1.070	0.078	0.023	4.9
PL/HW	0.793–0.899	0.840	0.035	0.010	2.8
PW/EL	0.422–0.478	0.443	0.023	0.007	3.4
PW/EW	1.120–1.280	1.180	0.071	0.021	4.0
PW/HW	0.880–0.978	0.930	0.033	0.010	2.3
EL/EW	2.520–2.750	2.670	0.082	0.024	2.0
EL/HW	1.980–2.170	2.100	0.074	0.022	2.3
EW/HW	0.734–0.837	0.786	0.041	0.012	3.5

Description.— Seta MP of frontale small. Meshes of microsculpture of parietale narrowly extended (7% of dorsal surface) from constriction behind eye toward occipital suture, and ventrally restricted to constriction behind eye; pointed microsculpture present baso-laterally on 5% of dorsal and ventral surface of parietale. Meshes of microsculpture absent from pronotum, and present on 20% of surface of mesonotum and metanotum; pointed microsculpture present near suture as a narrow band (7% of disc of mesonotum and on 15% of metanotum), restricted laterally (5% of surface of both nota), and absent from posterior band of both nota. Pointed microsculpture indistinctly outlined on urogomphus. Pointed microsculpture of membrane restricted on thorax (20% of ventral surface) and not extended to proepisternum, and present around hypopleuron of abdominal segments 2 to 7.

Second Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. clairvillei* by lack of meshes of microsculpture on pronotum, and of pointed microsculpture on ventral surface of abdominal membrane near sternites 2 to 7, and from larvae of *E. olivaceous* and *E. laevigatus* by presence of pointed microsculpture near suture of mesonotum and metanotum (2% and 10% of surface respectively), and on lateral portion of both nota (15% of surface).

Description.— Pointed microsculpture behind eye restricted (15% of dorsal surface and absent from ventral surface). Meshes of microsculpture absent from disc of pronotum, and present on 40% of surface of mesonotum. Pointed microsculpture near suture of mesonotum and metanotum (2% and 10% of disc respectively), and laterally on both nota (15% of surface). Mesepisternum and metepisternum without microsculpture. Pointed microsculpture on 10% of anterior band of tergum 9. Pointed microsculpture on membrane of abdominal segments 2 to 7 not reaching sternites and extended behind poststernites.

Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. clairvillei* by lack of pointed sculpture near suture of mesonotum, and by restricted development of pointed microsculpture

near suture of metanotum (3% of disc surface), and from larvae of remaining species of the group by pointed microsculpture extended over 60% of anterior band of tergum 9.

Description.— Meshes of microsculpture lacking on pronotum, and present on 40% of disc of mesonotum; pointed sculpture lacking near suture of mesonotum, restricted near suture of metanotum (3% of surface), and present laterally on both nota (10% of surface), on 5% of anterior and posterior bands of terga 1 to 8, and on 60% of anterior band of tergum 9. Abdominal sternite 9 with six accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends over most of boreal and cold temperate regions of the Palaearctic Region from the Atlantic coast of Europe (between arctic Scandinavia and Russia in the north, and France, northern Italy, Yugoslavia in the south), east across Siberia to northeastern China (Lindroth, 1945). I have seen specimens from Europe (Norway, Sweden, Finland, Denmark, Russia, Poland, Germany, England, Ireland, Holland, Belgium, France, Switzerland, Austria, Czechoslovakia and Hungary), east of the Caspian Sea (Geoktapa), and from northeastern China (Manchuria). Kryzhanovskij (*in litt.*) reported specimens of this species as far east as the Yakutsk and Lake Baikal regions.

Collecting notes.— Adults live on shaded wet organic mud flats where vegetation is scattered or lacking. These mud flats are near small rivers, large lakes, small pools, and in marshy areas of forests. Adults are lacking from pure inorganic soil, but occur on moss, though rarely on *Sphagnum* moss. Populations are known from the alpine zone of Norway and Finland but not from the arctic tundra (Lindroth, 1945:461).

Taxonomic notes.— Specimens of this species from northern Scandinavia are darker and match closely the description provided for *E. arcticus*.

I examined 500 adults and dissected six males. I studied three first instar, four second instar and two third instar larvae from Austria.

Geographical affinities.— This species is sympatric with *E. sibiricus,* a member of the *cupreus* group, and with *E. uliginosus, E. splendidus* and probably with *E. japonicus,* both members of the *uliginosus* group.

Elaphrus clairvillei Kirby

Figs. 50a-b, 73, 76a-g, 80, 82a-b, 85a-c, 90a-b, 96, 98a-c, 111, 122, 133,160, 162, 163, 164

Elaphrus clairvillei Kirby, 1837:61. Type locality: Lake Nipigon, Ontario (restricted by Lindroth, 1961); type (seen by Lindroth) in British Museum (Natural History), London. LeConte, 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Harrington, 1889:139. Blatchley, 1910:48. Hippisley, 1922:63. Guppy, 1947:51. 1948:76. Clark, 1948:25. Hatch, 1953:63. Lindroth, 1961:112.

Elaphrus politus LeConte, 1850:209; Type locality: Maple Island, Ontario (northwest of Sault Ste. Marie); Type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Lindroth, 1961:112.

Elaphrus frosti Hippisley, 1922:64. Type locality: Terrace, British Columbia; type not seen. Lindroth, 1961:112.

Elaphrus torreyensis Tanner, 1941:137. Type locality: Torrey, Wayne Co., Utah; type (seen by Lindroth, 1961) in Brigham Young University, Provo, Utah. Lindroth, 1961:112.

Elaphrus clairvillei var. *frosti*; Clark, 1948:25. Hatch, 1953:63.

Elaphrus clairvillei lynni Pierce, 1948b:52. Type locality: Lynne Creek, British Columbia; type (seen by me) in the Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

Adults

Diagnostic combination.— Distinguished from adults of *E. sibiricus* and *E. cupreus* by fused lateral ridges of elytral pits, thus the ridges are ring-shaped (Fig. 133). Distinguished from adults of remaining species by sparse punctures (10 to 120 microns apart) on pleura and

Table 12. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Fawcett, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.0–2.1	2.04	0.066	0.020	2.2
PW	2.1–2.3	2.21	0.114	0.034	3.4
EL	4.8–5.5	5.15	0.273	0.081	3.5
EW	1.7–2.0	1.88	0.094	0.028	3.3
HW	2.1–2.3	2.24	0.093	0.028	2.8
B. Proportions					
PL/PW	0.892–0.965	0.928	0.034	0.010	2.5
PL/EL	0.366–0.421	0.397	0.023	0.007	3.8
PL/EW	1.020–1.180	1.090	0.060	0.018	3.7
PL/HW	0.872–0.943	0.913	0.029	0.009	2.1
PW/EL	0.389–0.450	0.428	0.022	0.007	3.5
PW/EW	1.090–1.240	1.180	0.062	0.018	3.5
PW/HW	0.944–1.020	0.984	0.031	0.009	2.1
EL/EW	2.660–2.880	2.750	0.095	0.028	2.3
EL/HW	2.170–2.440	2.300	0.103	0.031	3.0
EW/HW	0.782–0.882	0.838	0.038	0.011	3.0

laterally on thoracic and abdominal sterna.

Description.— Upper body surface dark brassy-green or copper (boreal regions and along the Rockies), or darker and even black, elsewhere; pits purple, and postero-lateral angles of pronotum and impression of head bright metallic green in most specimens; ventral body surface black or black with brassy-green hue; legs reddish brown in most specimens from northeastern United States and adjacent areas of Canada, or dark brown, femora with metallic green hue, and dorsal surface of tibiae and tarsomeres purple.

Emargination of tooth of mentum 0.5 as deep as length of tooth. Pronotum with one pair of submedial impressions. Prosternal process with one to four accessory setae in about 50% of specimens. Metasternum with few punctures antero-medially; most punctures setose. Abdominal sterna 5 and 6 each with 15 to 25 accessory setae, sternum 7 with about 20 in males and five to 15 in females. Setigerous punctures of elytron sharply outlined. Pits of elytron deeply impressed, and with eight to 10 punctures near suture; lateral ridges of pits clearly fused anteriorly and posteriorly (Fig. 133), thus ring-shaped. Mirrors distinct on intervals 3 and 5, and slightly contrasted especially on dark specimens. Femur of foreleg with about 5 setae. Tibia of midleg of males with sharp projection at base of inner spur (Fig. 150). Hind coxa with punctures on outer 0.5 and with three to seven accessory setae near inner margin.

Integument sculpture. Punctures 20 to 25 microns in diameter on dorsal body surface, and 25 to 30 microns in diameter on ventral body surface. Punctures 20 to 75 microns apart on lateral portion of pronotum, 30 to 120 microns apart on intervals 4, 6 and 8 (Fig. 122), 50 to 60 microns apart on pleura, 20 to 180 microns apart on prosternum, five to 100 microns apart laterally on abdominal sterna, and 30 to 80 microns apart on coxae.

Meshes of microsculpture outlined in pits and impressions of pronotum very restricted elsewhere on dorsal body surface or not engraved. Microsculpture convex or subconvex on ventral body surface.

Male genitalia. Apex of median lobe in lateral view narrow, slightly spatulate, and slightly bent ventrally (Fig. 50b); in dorsal view moderately extended beyond apex of internal sac, thick-edged (40 to 60 microns) and markedly twisted (Fig. 50a).

Measurements and proportions.— Twenty-three samples studied, and data for three are presented in Tables 12 to 14.

Variation.— The most easily observed variation was color of the dorsal surface (Fig. 162). In northeastern United States and adjacent Canada adults are small, black, with rufous legs. In

Table 13. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Riverton, Manitoba.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.9–2.2	2.01	0.109	0.032	3.6
PW	1.9–2.3	2.12	0.138	0.041	4.4
EL	4.6–5.2	4.91	0.269	0.080	3.7
EW	1.6–1.9	1.76	0.114	0.034	4.3
HW	2.1–2.4	2.24	0.100	0.030	3.0
B. Proportions					
PL/PW	0.899–0.988	0.950	0.038	0.011	2.6
PL/EL	0.393–0.433	0.411	0.017	0.005	2.8
PL/EW	1.070–1.220	1.140	0.071	0.021	4.1
PL/HW	0.870–0.933	0.898	0.025	0.007	1.8
PW/EL	0.406–0.448	0.432	0.015	0.005	2.4
PW/EW	1.130–1.280	1.200	0.060	0.018	3.3
PW/HW	0.907–0.989	0.946	0.035	0.010	2.4
EL/EW	2.690–2.900	2.780	0.096	0.028	2.3
EL/HW	2.110–2.310	2.190	0.089	0.027	2.7
EW/HW	0.742–0.844	0.787	0.041	0.012	3.5

western Canada individuals are large, dark green with black legs. This last form also extends southward along the Rocky Mountains to Colorado and eastern Arizona. However, many smooth and dull specimens are mixed among a majority of more typical bright specimens in Utah and Colorado. The Arizona sample includes only dull individuals. The western Canadian form extends into British Columbia and eastern Alaska. West of the continental divide, specimens are darker green than east of there, and those of the Pacific coast are almost black. These data suggest a rather distinct eastern form, a clinal change along the Rocky Mountains from the boreal form to a dull southern form, and a slight differentiation in the Great Basin and Pacific coast regions.

An independent study of body proportions indicates more clearly this same pattern. I carefully chose 23 samples across the range of this species. The most consistent differences were between eastern United States (including adjacent Canada) and the remaining populations. Relative to central and western populations, eastern ones show significantly larger means for the ratios: PL/PW, PL/EL, PL/HW, PW/HW, EL/HW, EW/HW, and significantly smaller means for PL/EW (*i.e.*, eastern specimens have relatively narrower heads, longer pronota and wider elytra. See Figs. 163 and 164). However, some of these differences are less marked northward into southern Manitoba, northern Michigan and on the north shore of the gulf of the St. Lawrence River. The sample from Riverton, Manitoba, is intermediate between eastern and western forms. Thus, the eastern form intergrades with the western form in Manitoba, and probably so across northern Ontario and Quebec, although I have only small samples from that area. Surprisingly, specimens from Newfoundland are typical of the western form. If so, the Newfoundland population might have originated form the western form

Table 14. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Ridgewood, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8–2.1	1.98	0.159	0.036	2.0
PW	2.0–2.2	2.06	0.089	0.026	2.9
EL	4.3–4.9	4.63	0.232	0.069	3.3
EW	1.5–1.8	1.70	0.101	0.030	4.0
HW	2.0–2.3	2.25	0.111	0.033	3.3
B. Proportions					
PL/PW	0.931–1.000	0.963	0.022	0.006	1.5
PL/EL	0.417–0.453	0.428	0.015	0.004	2.3
PL/EW	1.110–1.260	1.170	0.050	0.015	2.8
PL/HW	0.860–0.951	0.882	0.032	0.009	2.4
PW/EL	0.428–0.465	0.445	0.016	0.005	2.4
PW/EW	1.150–1.290	1.210	0.049	0.015	2.7
PW/HW	0.889–1.000	0.916	0.038	0.011	2.8
EL/EW	2.640–2.830	2.730	0.097	0.029	2.4
EL/HW	1.930–2.250	2.060	0.107	0.032	3.4
EW/HW	0.697–0.827	0.755	0.046	0.024	4.1

spreading across Quebec. If not, it may be a relic population. Interpopulational differences in the western form are generally inconsistent. Samples from southern boreal regions (Cypress Hills, Alberta; Churchill, Manitoba; and Newfoundland) and cold grassland (Williams Lake, British Columbia) are similar to those from Colorado and the Great Basin (including the sample from southcentral British Columbia). The sample from eastern Arizona is most similar to that of Colorado, but is consistently different from this and samples of the Great Basin in having a significantly larger mean for ratio PW/HW. The only other significantly different populations are the adjacent samples from southcentral British Columbia and Terrace, British Columbia with those from boreal British Columbia. The first two samples are basically similar to samples south of these localities, but are consistently different from boreal samples with significantly smaller means for ratios PW/HW, EL/HW and EW/HW (*i.e.*, the head is relatively wider). Though these results suggest lack of gene flow between the boreal form and the form south of it, the data on variation suggest gene flow between the Great Basin and Colorado populations and the boreal regions by the Great Basin-Rocky Mountain arc. Samples from western North America (eastern Alaska, northernmost British Columbia, southern Yukon, and northcentral Alberta) show significantly larger means for ratio EW/HW. Most samples also show significantly larger means for ratios PW/HW, EL/HW and PW/EW. These differences are most pronounced in eastern Alaska. Therefore, there is evidence for clinal variation and for gene flow between northwestern populations and other southern and eastern boreal populations.

In summary, I recognize a boreal, a western (Great Basin and Pacific Coast), and a New England (including adjacent Canada) form, but gene flow is apparently uninterrupted between

them. Therefore, I do not consider it necessary to recognize subspecies.

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. cupreus* by widespread meshes of microsculpture of parietale dorso-laterally (20% of surface), and from larvae of remaining species of the group by lack of microsculpture on the disc of pronotum, and by restricted pointed microsculpture ventrally on thoracic membrane (15% of surface).

Description.— Seta MP of frontale small. Meshes of microsculpture of parietale widespread dorso-laterally (20% of surface), and restricted ventro-laterally (2% of surface). Meshes of microsculpture absent from pronotum, and present on 20% of surface of mesonotum and 30% of surface of metanotum; pointed microsculpture moderately restricted near suture (7% of disc of mesonotum and 15% of disc of metanotum), restricted laterally (5% of surface of both nota), and absent from posterior bands of these nota. Pointed microsculpture clearly outlind on urogomphus. Pointed microsculpture of membrane restricted on thorax (20% of ventral surface) and not extended to proepisternum, and expanded around hypopleuron of abdominal segments 1 to 8.

Second Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. cupreus* by presence of meshes of microsculpture on 10% of pronotum, and of pointed microsculpture on membrane reaching abdominal sternites 2 to 7, and from remaining species of the group by presence of pointed microsculpture near suture of mesonotum and metanotum (2%, and 10% of disc respectively), and on anterior band of tergum 9 (10% of band surface).

Description.— Pointed microsculpture moderately restricted dorso-laterally (15% of surface), and absent ventro-laterally. Meshes of microsculpture present on 10% of surface of pronotum, on 40% of surface of mesonotum and metanotum. Pointed microsculpture restricted near suture of mesonotum and metanotum (2% and 10% of disc respectively), and laterally on both nota (15% of surface). Mesepisternum and metepisternum without microsculpture. Pointed microsculpture present on 10% of anterior band of tergum 9. Pointed microsculpture of membrane of abdominal segments 2 to 7 reaching sternite and expanded behind poststernites.

Third Instar Larvae

Diagnostic combination.— distinguished from larvae of *E. cupreus* by presence of pointed microsculpture near suture of mesonotum and metanotum (10% of surface), and from other species of the group by presence of pointed microsculpture on lateral portion of mesonotum and metanotum, and on 60% of anterior band of tergum 9.

Description.— Meshes of microsculpture lacking on pronotum, and present on 40% of surface of mesonotum; pointed microsculpture present near suture of mesonotum and metanotum (10% of disc), on lateral portion (10% of disc), on 5% or more of anterior and posterior bands of terga 1 to 8, and on 60% of anterior band of tergum 9. Abdominal sternite 9 with six accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends throughout cold temperate and boreal regions of North America, from Alaska to Newfoundland as far north as treeline, and as far south as northern New England in the east and northern California in the west. Along the Rocky Mountains the range of *E. clairvillei* extends south to Colorado and the White Mountains of eastern Arizona (Fig. 160).

Collecting notes.— Adults live on soft wet organic mud in the shade of sedges (*Carex* and *Amblystegium* vegetation), or taller vegetation (*Typha* and *Alnus*), or forest canopy. Females oviposit from mid-May until late July. Immatures are common in June, and larvae of all three instars can be found together in July. I found pupae in rotten logs. Though development is rapid, teneral adults do not appear until the end of July, thus emergence seems synchronized. Teneral and older adults are seen until the end of September. Thereafter, most adults are found

in forest litter where the soil is naturally well drained, or under bark of old logs that are well above flood level. Only adults overwinter. During the first half of May adults return to marshes. Adults are diurnal and can live for at least two summers (*i.e.*, many females are found in early May with large *corpora lutea*). Larvae live in the same general habitat of adults, but are mostly within soil. Adults are opportunistic feeders, and eat soft-bodied animals. I have not observed predatory behaviour among adults, but larvae attack small arthropods of any type, including each other under laboratory conditions despite abundance of food.

Taxonomic notes.— Types of named, conspecific form match typical specimens of population at or near approximate type localities. *E. clairvillei lynni,* a fossil, known from an elytron is a typical adult of *E. clairvillei* as shown by circular ridges around elytral pits, and puncture development in elytral pits and on intervals 4, 6 and 8. This specimen matches extant specimens near the type locality.

I studied more than 1500 adults and dissected more than 100 males. I examined seven first instar, five second instar, and four third instar larvae from George Lake, Alberta.

Geographical affinities.— The range of this species overlaps that of *olivaceus,* and perhaps in northeastern California, that of *E. laevigatus,* both members of the *cupreus* group. Its range is also sympatric with those of *E. fuliginosus* and *E. cicatricosus* in eastern North America.

Elaphrus olivaceus LeConte

Frontispiece and Figs. 51a-b, 123, 134, 161, 165, 166, 167

Elaphrus olivaceus LeConte, 1863:1. Type locality: Catskill Mountains, New York; type not seen. Crotch, 1873:4. 1876:246. Schaupp, 1878:6. Lindroth, 1961:113.

Adults

Diagnostic combination.— Distinguished from adults of other species of this group by brown antennomeres 1 to 3, and by very fine, dense and widespread punctures on metasternum and hind coxae. Otherwise, dorsal body surface similar to that of *E. pyrenoeus* of the *uliginosus* group.

Description.— Upper body surface green (bright emerald to olive), blue green, dark brown olive, or reddish brown except for purple pits; ventral body surface dark golden-green or copper; legs, palps and antennomeres 1 to 3 rufous, femora with green or copper hue, apex of tibiae and tarsomeres metallic green or copper on dorsal surface.

Emargination of tooth of mentum 0.2 to 0.25 as deep as length of tooth. Pronotum with two pairs of discal impressions. Prosternal process without accessory setae. Metasternum densely punctate antero-medially; about 20% of punctures with setae. Abdominal sterna 3 and 4 each with 10 to 20 accessory setae, sterna 5, 6 and 7 (in both sexes) each with less than three (Fig. 139). Setigerous punctures on elytron clearly outlined. Elytral pits not deeply impressed, and with eight to 15 punctures; lateral ridges narrow or not distinct, and apparently fused anteriorly and posteriorly (Fig. 134). Mirrors indistinctly outlined on intervals 3 and 5, and weakly contrasted against microsculpture-free intervals 4, 6 and 8. Femur of foreleg with about 20 setae. Tibia of midleg of males without projection at base of inner spur. Hind coxae densely punctate over surface and with two to five accessory setae along inner margins.

Integument sculpture. Punctures 15 to 20 microns in diameter on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123), 25 to 30 microns in diameter on pleura, lateral portions of thoracic and abdominal sterna, and on coxae. Punctures 10 to 20 microns apart on head, lateral portion of pronotum, elytral intervals 4, 6 and 8, and on pleura and abdominal sterna, 5 to 50 microns apart on thoracic sterna and coxae.

Meshes of microsculpture absent from head, pronotum (except postero-lateral angles and lateral portion), and elytron (except in pits and near shoulder. See Fig. 134). Microsculpture flat on lateral portion of pronotum, near shoulder, on thoracic sterna, propleuron and mesopleuron; convex or subconvex on metapleuron, abdomen, postero-lateral impressions of pronotum, and elytral pits.

Male genitalia. Apex of median lobe in lateral view narrow (Fig. 51b); in dorsal view shortly extended posterior to apex of internal sac, thin-edged (20 microns wide) and straight (Fig. 51a).

Measurements and proportions.— Seven samples studied, and data for three are presented in Tables 15 to 17.

Table 15. Descriptive statistics for *E. olivaceus* based on two males and four females from Central Colorado: Fairplay, Santa Maria, Plum Creek, Bellevue.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.6–1.8	1.72	0.087	0.047	3.4
PW	1.8–1.9	1.85	0.050	0.027	1.8
EL	3.8–4.2	4.08	0.215	0.117	3.5
EW	1.4–1.6	1.49	0.117	0.064	5.2
HW	1.9–2.0	1.92	0.050	0.027	1.7
B. Proportions					
PL/PW	0.904–0.973	0.928	0.027	0.020	2.7
PL/EL	0.411–0.429	0.422	0.011	0.006	1.7
PL/EW	1.110–1.200	1.150	0.058	0.031	3.3
PL/HW	0.846–0.936	0.896	0.045	0.024	3.3
PW/EL	0.441–0.474	0.455	0.017	0.009	2.4
PW/EW	1.190–1.330	1.240	0.081	0.044	4.3
PW/HW	0.936–1.000	0.965	0.031	0.017	2.2
EL/EW	2.650–2.810	2.730	0.102	0.055	2.5
EL/HW	1.970–2.210	2.120	0.128	0.069	4.0
EW/HW	0.705–0.813	0.779	0.064	0.035	5.5

Variation.— Adults from Colorado, Alberta and eastern North America, at first glance, are similar. However, populations from these regions differ in the number of different color forms (see Fig. 165). In coastal New England there are two color forms: blue-green and olive. In interior New England (*i.e.,* Green Mountains, Vermont and Adirondack Mountains, New York) these two forms co-exist with a third dark brown form with green punctures. This last form is not discrete because specimens between this and the olive form exist. In boreal Québec, on the north shore of the St. Lawrence River (St. Fidèle), the brown form with golden punctures is discrete. From this last locality to Medicine Hat, Alberta, I have seen specimens of these three color forms. Westward the brown form with golden punctures turns reddish brown. In central and northern Alberta, I collected only two color forms: olive and red-brown. This last form has copper punctures. From Newfoundland I have two forms: olive and blue-green, and from Colorado only olive specimens. However, these two samples are too small to determine the range of color forms. These results suggest a cline from east to west in the formation and differentiation of a third color form. Three forms exist from eastern Canada to Medicine Hat, Alberta, but only two in central Alberta. Thus, there is a suggestion of a break in gene flow, but the reddish-brown form, though distinct, is nevertheless most similar to the brown form from Medicine Hat. Therefore, gene flow might still exist in areas of either the Rocky Mountain foothills or the boreal regions of Saskatchewan and Manitoba that have not been adequately sampled.

In an attempt to clarify this problem, I studied variation in body proportions of adults of carefully chosen samples from across the range of this species. Results confirmed and completed the general picture presented above. The Colorado sample showed the lowest mean

Table 16. Descriptive statistics for *E. olivaceus* based on 10 males and 10 females from Flatbush, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.81	0.108	0.032	4.0
PW	1.7–2.0	1.83	0.111	0.033	4.0
EL	4.0–4.6	4.23	0.266	0.079	4.2
EW	1.4–1.7	1.55	0.134	0.040	5.7
HW	1.8–2.1	1.93	0.091	0.027	3.1
B. Proportions					
PL/PW	0.946–1.040	0.993	0.047	0.014	3.2
PL/EL	0.403–0.455	0.430	0.023	0.007	3.6
PL/EW	1.070–1.290	1.170	0.080	0.024	4.6
PL/HW	0.900–0.974	0.937	0.034	0.010	2.4
PW/EL	0.407–0.462	0.433	0.022	0.007	3.4
PW/EW	1.090–1.260	1.180	0.073	0.022	4.2
PW/HW	0.909–1.000	0.944	0.073	0.010	2.4
EL/EW	2.580–2.860	2.720	0.100	0.030	2.4
EL/HW	2.100–2.290	2.180	0.083	0.025	2.5
EW/HW	0.747–0.857	0.813	0.046	0.014	3.8

values for ratios PL/PW and PL/EL (*i.e.*, the pronotum is relatively short. See Fig. 166). This sample is most similar to that of central Alberta, and most different from that of Medicine Hat, Alberta. The central Alberta sample is consistently different from all more eastern samples with its significantly larger mean for ratio EL/HW. It also differs significantly from most eastern samples in its mean for each of the following ratios: PL/HW, PW/HW and EW/HW (*i.e.*, the head is relatively narrower. See Fig. 167). The central Alberta sample is most similar to that of Medicine Hat, and increasingly different from samples eastward. The sample from a locality east of Medicine Hat most similar to the western samples is from southern Manitoba, and the most different samples are those from New Brunswick and Newfoundland. The progressively more extensive differentiation of the Medicine Hat sample from more easterly samples suggests gene flow between eastern and western complexes, and among the latter samples. Samples of the eastern complex (Manitoba to Newfoundland) are generally similar to one another in the features studied.

The data suggest basically three forms: one from Colorado, another from northern Alberta, and a third extending from Medicine Hat, Alberta, eastward. However, the Medicine Hat sample is both most proximate and most similar to the Colorado and Northern Alberta samples. Although more specimens are needed from the Rocky Mountain area and the northern Prairie provinces, the data suggest that gene flow takes place among these populations. Therefore, I do not consider it appropriate to recognize subspecies.

Table 17. Descriptive statistics for *E. olivaceus* based on 11 males and 9 females from Medicine Hat, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.7–2.0	1.82	0.145	0.043	5.3
PW	1.7–2.0	1.87	0.144	0.043	5.1
EL	3.6–4.6	4.17	0.387	0.115	6.2
EW	1.3–1.7	1.53	0.159	0.047	6.9
HW	1.7–2.1	1.96	0.126	0.037	4.3
B. Proportions					
PL/PW	0.921–1.030	0.975	0.034	0.010	2.3
PL/EL	0.415–0.479	0.439	0.022	0.006	3.3
PL/EW	1.120–1.270	1.190	0.061	0.018	3.4
PL/HW	0.875–0.964	0.929	0.039	0.011	2.8
PW/EL	0.425–0.500	0.450	0.026	0.008	3.8
PW/EW	1.150–1.330	1.220	0.066	0.020	3.6
PW/HW	0.913–1.000	0.951	0.042	0.013	3.0
EL/EW	2.640–2.830	2.710	0.076	0.023	1.9
EL/HW	1.900–2.260	2.120	0.115	0.034	3.6
EW/HW	0.714–0.840	0.781	0.044	0.013	3.7

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. laevigatus* by restricted pointed microsculpture on parietale behind eye (5% of dorsal and 3% of ventral surfaces), and from larvae of remaining species of the group by the presence of meshes of microsculpture on pronotum (5% of surface), by the extended pointed microsculpture on ventral surface of thoracic membrane (45% of surface), by the very fine pointed microsculpture of urogomphi, and by the restricted pointed microsculpture on the base of abdominal sternite 10.

Description.— Seta MP of frontale very small. Meshes of microsculpture of parietale expanded baso-laterally (50% of dorsal surface) and ventro-laterally; pointed microsculpture restricted to constriction behind eye (5% of dorsal surface and 3% of ventral surface). Meshes of microsculpture present on 5% of disc of pronotum, and on 40% of surface of mesonotum and metanotum; pointed miscrosculpture of mesonotum and metanotum widespread near suture (20% of surface), restricted laterally (5% of surface), and absent from posterior band. Pointed microsculpture clearly outlined on urogomphus. Pointed microsculpture of membrane expanded on thorax (40% of surface), and extended to proepisternum, and extended around hypopleuron of abdominal segments 2 to 7.

Second Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. laevigatus* by the restricted pointed microsculpture behind eye (15% of dorsal and 3% of ventral surface of parietale). Distinguished from larvae of remaining species of the group by lack of pointed microsculpture from mesonotum and metanotum, and from the anterior band of tergum 9.

Description.— Pointed microsculpture behind eye restricted (15% of dorsal surface and 3% of ventral surface of parietale). Meshes of microsculpture present on 30% of surface of pronotum, and on 40% of surface of mesonotum. Pointed microsculpture absent from mesonotum and metanotum. Mesepisternum and metepisternum without sculpture. Pointed microsculpture absent from anterior band of tergum 9. Pointed microsculpture of abdominal membrane extended around

hypopleura and behind poststernites.

Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. laevigatus* by presence of meshes of microsculpture on 10% of disc of pronotum, and on 40% of disc of mesonotum and metanotum, and from those of remaining species of the group by absence of pointed microsculpture from mesonotum and metanotum, and anterior band of tergum 9.

Description.— Meshes of microsculpture present on 10% of pronotum and 40% of surface of mesonotum and metanotum; pointed microsculpture absent from nota, anterior band of tergum 9, and posterior band of terga 1 to 8. Abdominal sternite 9 with two accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends across the southern boreal and cold temperate regions of North America, from central British Columbia to Newfoundland south to New Jersey and along the Rocky Mountains to Colorado (Fig. 161).

Collecting notes.— Adults live on soft or firm organic mud flats exposed to sunlight. In Massachusetts these beetles were common in *Typha* marshes on sun-exposed ground. On the north shore of the St. Lawrence River I found many specimens on firm brown mud among scattered clumps of *Carex nigra.* In Gatineau Park, Quebec, I found them on the fine soft muds of an abandoned beaver pond. In Alberta, adults and larvae are commonly obtained from *Carex* swamps near the *Typha* zone where clumps of *Carex rostrata are* sparser, and where thin brown mosses are found above water. An excellent method to concentrate these beetles was to cultivate the *Carex* zone into a clean black organic mud flat. This heliophilous species has a life cycle similar to that of *E. clairvillei.* However, I do not know where adults of *E. olivaceus* overwinter.

Taxonomic notes.— I have examined about 1100 adults and dissected 10 males. I studied five first instar, two second instar, and 10 third instar larvae from George Lake, Alberta.

Geographical affinities.— This species occurs sympatrically with *E. clairvillei,* a member of the *cupreus* group, and also with *E. fuliginosus* and *E. cicatricosus,* both members of the *fuliginosus* group.

Elaphrus laevigatus LeConte
Figs. 52a-b, 161

Elaphrus laevigatus LeConte, 1852:200. Type locality: San Fancisco, California; type (seen by me) in the Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:402. Crotch, 1873:4. 1876:246. Schaupp, 1878:5. Blatchley, 1910:48. Van Dyke, 1925:113. La Rivers, 1946:138. Hatch, 1953:63 Lindroth, 1961:113.

Elaphrus politus Casey, 1897:345 (junior homonym of *E. politus* LeConte, 1850). Type locality: San Francisco, California; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington. D.C. Van Dyke, 1925:113. Lindroth, 1961:113.

Elaphrus caseyi Leng, 1918:203. New name for the junior homonym proposed by Casey, 1897.

Adults

Diagnostic combination.— Distinguished from specimens of other species of this group by sparse dorsal punctures (10 to 200 microns apart), and by dense ventral punctures on pleura (5 to 20 microns apart).

Description.— Upper body surface black except for blue-green postero-lateral impressions of pronotum, pits and punctures; ventral surface black with faint metallic golden-green hue; legs and palpi piceous, femora with metallic blue-green hue, and dorsal surface of tibia and tarsomeres with metallic purple hue.

Table 18. Descriptive statistics for *E. laevigatus* based on 10 males and 10 females from San Francisco Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.6–1.8	1.71	0.098	0.029	3.8
PW	1.8–2.0	1.89	0.116	0.035	4.1
EL	3.9–4.4	4.14	0.240	0.071	3.9
EW	1.3–1.6	1.46	0.115	0.034	5.3
HW	1.7–2.0	1.89	0.113	0.034	4.0
B. Proportions					
PL/PW	0.868–0.973	0.905	0.040	0.012	2.9
PL/EL	0.400–0.450	0.414	0.017	0.005	2.8
PL/EW	1.110–1.330	1.180	0.074	0.022	4.2
PL/HW	0.875–0.960	0.907	0.032	0.009	2.3
PW/EL	0.439–0.475	0.458	0.012	0.003	1.7
PW/EW	1.250–1.410	1.300	0.058	0.017	3.0
PW/HW	0.973–1.060	1.000	0.034	0.010	2.2
EL/EW	2.750–2.960	2.840	0.090	0.027	2.1
EL/HW	2.120–2.290	2.190	0.073	0.022	2.2
EW/HW	0.720–0.797	0.772	0.032	0.010	2.8

Emargination of tooth of mentum half as deep as length of tooth. Pronotum with one pair of submedial impression. Intercoxal process of prosternum without accessory setae. Antero-medial surface of metasternum with few punctures; most punctures with setae. Abdominal sterna 5 and 6 with about 10 accessory setae, sternum 7 in males with 10 to 20 setae and in females with about five. Setigerous punctures of elytron indistinctly outlined. Pits of elytra deeply impressed, and with four or five punctures; lateral ridges of pits wide and fused anteriorly and posteriorly. Mirrors indistinctly outlined and not contrasted against brilliant intervals 4, 6 and 8. Femur of foreleg and midleg with about 40 setae. Tibia of midleg of males without projection at base of inner spur. Hind coxae with few outer punctures and three to five accessory setae near inner margin.

Integument sculpture. Punctures 10 to 25 microns in diameter on clypeus, head, pronotum, on elytral intervals 4, 6 and 8, and on coxae; 25 to 30 microns in diameter on pleura and lateral portions of thoracic and abdominal sterna. Punctures 10 to 200 microns apart on pronotum, about 60 microns apart at base of head, five to 20 microns apart on pleura, and 25 to 100 microns apart on lateral portion of thoracic and abdominal sterna.

Microsculpture flat in postero-lateral impressions of pronotum and in elytral pits, absent from most of dorsal body surface, flat ventrally.

Male genitalia. Apex of median lobe in lateral view moderately widened near internal sac. (Fig. 2); in dorsal view apex shortly extended posterior to base of internal sac, thin-edged (20 microns wide) and straight (Fig. 52a).

Measurements and proportions.— Two samples studied, with one presented in Table 18.

Variation.— A sample from localities near San Francisco shows smaller means for measurements than that from northeastern California. Specimens from northeastern California have relatively wide elytra (ratios: EL/EW = 2.73, and EW/HW = 0.805).

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. olivaceus* by widespread microsculpture on baso-lateral portion of parietale (50% of dorsal surface and 15% of ventral surface), and from larvae of other species by presence of meshes of microsculpture on the pronotum.

Description.— Seta MP of frontale very small. Pointed microsculpture widespread laterally on parietale (50% of dorsal surface and 15% of ventral surface). Meshes of microsculpture present on 10% of surface of pronotum, and on 50% of surface of mesonotum; pointed microsculpture of mesonotum and metanotum moderately widespread near suture (10% of disc), widespread laterally (35% of disc), and on 60% of surface of posterior band. Pointed microsculpture of urogomphus distinctly outlined. Pointed microsculpture of membrane moderately widespread on thorax (30% of ventral surface) and clearly extended to proepisternum, and restricted on abdomen to epipleura.

Second and Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. olivaceus* by widespread microsculpture on parietale especially behind eye (50% of dorsal surface and 10% of ventral surface), and from larvae of remaining species of the group by absence of pointed microsculpture near suture of mesonotum and metanotum, and from anterior band of tergum 9.

Second Instar Larvae

Description.— Pointed microsculpture of parietale widespread baso-laterally (30% of dorsal surface and 5% of ventral surface). Meshes of microsculpture on 75% of surface of pronotum, on 90 to 100% of surface of mesonotum. Pointed microsculpture present laterally on mesonotum (10% of surface) and absent near suture. Mesepisternum and metepisternum with fine multi-pointed microsculpture. Pointed microsculpture absent from anterior band of tergum 9. Pointed microsculpture of abdominal membrane not extended around hypopleuron.

Third Instar Larvae

Description.— Meshes of microsculpture present on 75% of surface of pronotum, and 90 to 100% of surface of mesonotum; pointed microsculpture absent from lateral portion of mesonotum and metanotum, present on 5% or more of anterior band of terga 1 to 8, absent from posterior band of terga 1 to 8 and anterior band of tergum 9. Abdominal sternite 9 with two accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends from northern California as far south as Los Angeles area, and as far east as Reno, Nevada (Fig. 161).

United States. CALIFORNIA (4;ANSP, UMRM, DEFW, AMNH): Hullville (2;MCZC); Alameda Co. (3;KSUC, FMNH); Oakland (1;CASC); Fresno Co., Fresno (1;ICCM); Kern Co., Mill Portrero (1;LACM); Lassen Co., Norvell--misspelled Norval (1;CASC); Warner Valley, Lassen National Forest (1;CASC); Los Angeles Co., Claremont (1;CUIC); Madera Co., Chiquito Creek, 4100'(2;CUIC, USNM); North Fork--misspelled Northfork (3;CUIC, USNM); Marin Co., Inverness (1;CASC), Tamales Bay (1;CASC); Monterey Co., Carmel (3;CASC, UASM), Monterey (2;CASC); Plumas Co., 6 mi, n.w. Chester (1;USNM); 4 mi. w. Quincy (1;UCRC); San Francisco Co., (42;USNM, CASC, MCZC, SEMC), San Francisco (22;USNM, CASC, ANSP, PURC); San Luis Obispo Co., San Luis Obispo (1,FMNH); Sonoma Co., Eldridge (1;CASC); Siskiyou Co., (2;CASC); Trinity Co., Carrville (5;CASC); Tuolumne Co., (1,CASC). NEVADA: Washoe Co., Reno (1;MCZC). NEW YORK: Barre– no doubt mislabelled (1;CUIC).

Collecting notes.— Adults of this species live on soft black mud under dead and dense *Juncus*-like vegetation. This habitat is in the shade of deciduous and broad-leaf evergreen trees during the day, and is similar to that described for *E. clairvillei*. Oviposition took place in the laboratory soon after obtaining adults in April. I saw a teneral adult collected in late September in Warner Valley, Lassen Co., therefore, in northeastern California populations probably overwinter as adults.

Taxonomic notes.— I examined 130 adults and dissected 4 males. I studied six first instar, five second instar, and five third instar larvae from San Francisco, California.

Geographical affinities.— Allopatric, but probably sympatric in northeastern California with *E. clairvillei,* a member of the *cupreus* group.

Subgenus *Elaphrus* Fabricius

Elaphrus Fabricius, 1775:227. Type-species: *Cicindela riparia* Linnaeus, 1758, fixed by Latreille (1810), by subsequent

designation, Hatch, 1951:113. 1953:63; Ball, 1960:106. Lindroth, 1961:114. Nakane *et al.*, 1963: 19.

Elaphroterus Semenov, 1895:309. 1904a:19. Jacobson, 1906:267. Reitter, 1908:96;97. 1909:104. Bänninger, 1919:149. Porta, 1923:78. Portevin, 1929:41. All *ex parte*.

Trichelaphrus Semenov, 1926:39. Type-species: *Cicindela riparia* Linnaeus, 1758, fixed by Semenov, (1926), by original designation. Bänninger, 1931:184. Jeannel, 1941:216.

Adults

Diagnostic combination.— Distinguished from adults of other subgenera as in following. Clypeus with two pair of setae. Trochanter of foreleg and midleg with three setae. Setae covering hind coxa. Process of mesosternum setose.

Description.— *Head.* Frons without medial impression (though suggested by elongate punctures and by irregular carinae). Clypeus with two pairs of setae. Terebral margin of right mandible more than 0.5 of mandible length; basal tooth of retinaculum entire, and apex of retinacular tooth near terebral tooth (Fig. 4).

Thorax. Lateral margin of pronotum beaded except in sinuation (completely beaded in adults of *E. marginicollis*). Fringe of setae along posterior margin of pronotum reaching hind angles; setae of fringe scimitar-shaped and enlarged apically. Proepimeron and proepisternum apparently fused. Prosternum setose. Process of mesosternum setose; postero-lateral ridge of mesosternum absent.

Abdomen. Tergum 7 without setae except on stridulatory scrapers.

Elytra. Striae lacking. Transverse basal stria slightly expressed at shoulder. Setigerous punctures of elytron 40 to 50 microns in diameter. First sutural mirror wide, others narrower (except in some individuals of *E. viridis*). Elytral pits with 50 to 200 regularly distributed punctures (Figs. 20 to 25).

Legs. Foreleg: trochanter with three setae; femur with 60 to 85 setae; tibia with 25 to 45 setae; inner dorsal fringe 0.7 to 0.75 as long as tibia, and without setae posteriorly; first three tarsomeres of males with ventral spongy pubescence. Midleg: trochanter with three setae; femur with 60 to 95 setae; tibia with 65 to 115 setae. Hindleg: coxa with setae covering surface; femur with 24 to 31 setae; tibia with 70 to 95 setae.

Male genitalia. Internal sac of median lobe without scales posteriorly.

Ovipositor. Basal sclerite of stylus without apico-ventral setae; apical sclerite with two to six lateral stout setae on dorso-medial and dorso-lateral ridges, apex without setae (Fig. 75).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other subgenera as in following. Seta EA-E on frontale very small. Epicranial suture small, less than 0.7 length of antennal scape. Outer surface of stipes with membranous declivity behind postero-lateral seta, outer margin straight; postero-lateral pores proximate (Fig. 83b).

First Instar Larvae

Description.— Medial point of nasale acute; teeth of nasale absent or extremely fine, and ending at base of medial point (Fig. 91). Setae Ea-E of parietale very small. Epicranial suture less than 0.7 as long as antennal scape. Head short; bisinuation of lateral margin behind eye with anterior and posterior convexity subequal. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 90° to 110°. Triangle formed by setae DEP, VEP-P and VEM-P on parietale short (anterior angle open). Pointed microsculpture absent from ventral surface of parietale. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin straight (Fig. 83b); dorsal surface with about 30 setae on inner half, subapical setae roughly distributed in two rows; postero-ventral pores proximate (Fig. 83b). Pronotum covered with meshed microsculpture, pointed microsculpture present on 3 to 5% of surface. Pointed microsculpture absent from surface of anterior band of terga 1 to 8.

Second Instar Larvae

Description.— Outer margin of stipes behind postero-lateral seta projected outward. Each sclerite of pronotum and mesonotum with about 15, and eight to 10 accessory setae respectively; pointed microsculpture present on 30 to 40% of anterior band of mesonotum. Each sclerite of terga 1 to 8 with seven to nine accessory setae. Basal major accessory seta of urogomphus near middle; pointed sculpture present on entire band surface of terga 1 to 9, and on entire posterior band of terga 1 to 8. Hypopleuron of segments 1 to 8 with about four accessory setae.

Third Instar Larvae

Description.— Each sclerite of mesonotum with 23 to 25 accessory setae, and mesonotal epipleuron with one accessory seta. Mesepimeron with fewer than three accessory pores. Largest projection of urogomphus in lateral view large (Fig. 100b). Sclerite of terga 1 to 8 each with 17 to 20 accessory setae. Epipleuron of abdominal segments 2 to 8 with eight to 14 accessory setae. Hypopleuron of abdominal segment 1 to 8 with eight to 10 accessory setae. Sternite of abdominal segment 1 with four to eight accessory setae, those of segments 2 to 7 each with 12 to 20, that of segment 8 with 14 to 20, that of segment 9 without or up to four, and that of segment 10 with five or less. Inner poststernites each with one to two accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of species of this subgenus extends across Palaearctic and Nearctic Regions, from the southern edge of the tundra to the southern edge of the warm temperate Zone.

Key to the species of subgenus *Elaphrus* Fabricius

Adults

1 Lateral margin of pronotum clearly beaded in sinuation (Fig. 20). Puncture 40 to 50 microns in diameter on pronotum, and 25 microns in diameter on elytra. Western Nearctic Region ..... *E. marginicollis* new species p. 288

1′ Lateral margin of pronotum not beaded in sinuation (Figs. 21 and 25). Puncture 20 to 30 microns in diameter on pronotum and elytra 2

2 (1′) Lateral margin of pronotum explanate near middle and projected (best seen in lateral view) (Figs. 77a, 77b, 77c). Punctures of pronotum almost as dense submedially as antero-laterally. Main mirror near suture roughly ovate (Figs. 114, 115, 126 and 127) 3

2′ Lateral margin of pronotum not explanate near middle and not projected (Fig. 77d). Punctures of pronotum twice as dense submedially as antero-laterally. Main mirror of most specimens rectangular (Figs. 116, 117, 128 and 129) 5

3 (2) Elytral pits large: intervals 4, 6 and 8 almost absent and much disrupted (Figs. 115 and 127). Accessory setae present on pronotum only (Fig. 105). Pronotum with many impressions on disc (Fig. 105). Frons with medial impression. Morocco and Spain ..... *E. lheritieri* Antoine p. 290

3′ Elytral pits absent (Figs. 114 and 126) or relatively small: intervals 4, 6 and 8 wide and almost straight (Figs. 116 and 128). Accessory setae present on head and pronotum (Fig. 105). Pronotum not impressed except near hind angle (Fig. 106). Frons without medial impression. California 4

4 (3′) Elytral pits absent (Figs. 114 and 126). Punctures of dorsal surface 5 to 10 microns apart. Accessory setae abundant and long on head and pronotum (Fig. 106). Accessory setae on at least abdominal sternum 5 extended laterally to punctate area (Figs. 143 and 144). Dorsal surface brilliant metallic green ..... *E. viridis* Horn p. 291

4′ Elytral pits clearly developed (Figs. 116 and 128). Punctures of pronotum 10 to 20 microns apart. Accessory setae sparse and short on head and pronotum. Accessory setae on abdominal sterna not extended laterally to

punctate area (Fig. 140). Dorsal surface dark green ..... *E. mimus* new species p. 290

5 (2′) Abdominal accessory setae extended at least to edge of fifth sternum (Figs. 141 to 144) 11

5′ Abdominal accessory setae not extended to edge of sterna -- on most specimens between ambulatory setae and punctate area (Fig. 140) 6

6 (5′) Punctures of proepisternum 20 to 40 microns apart (Fig. 109). Third visible sternum with 40 to 60 punctures on each side (Fig. 141). Males and females with similar abundance of accessory setae on abdominal sterna 7

6′ Punctures of proepisternum 10 to 25 microns apart. Abdominal sternum 3 with 100 to 200 punctures on each side (Fig. 140). Most females with fewer accessory setae on abdominal sterna than males. Nearctic Region 8

7 (6) Punctures on proepisternum large (50 to 60 microns in diameter), surface around them depressed (Fig. 109); surface of proepisternum almost black: microsculptured surfaces dark copper and punctures dark blue-green. Eastern Nearctic Region ..... *E. ruscarius* Say p. 293

7′ Punctures of proepisternum 30 to 40 microns in diameter, surface around them barely or not depressed; surface of proepisternum metallic: microsculptured surfaces copper and punctures green. Western China or adjacent U.S.S.R. ..... *E. hypocrita* Semenov p. 293

8 (6′) Pronotum enlarged at middle (Fig. 24); anterior transverse impression sharply impressed toward antero-lateral angle. Antennomere 3 with 30 to 40 setae (Fig. 13) -- most setae on posterior surface. Prairie regions of Nearctic Region ..... *E. lecontei* Crotch p. 295

8′ Pronotum slightly enlarged at middle (Fig. 25); anterior transverse impression not impressed. Antennomere 3 without or with less than 20 accessory setae (Figs. 11, 12) 9

9 (8) Hind femur, dorsal aspect with three to seven long (100 to 150 microns) white setae subapically (Fig. 35). Elytra strongly constricted in basal 0.3 – less evident in females. Nearctic Region ..... *E. californicus* Mannerheim p. 299

9′ Hind femur, dorsal aspect with one (rarely two or three) short (40 to 80 microns) white setae subapically (Fig. 34). Elytra slightly constricted in basal 0.3 10

10 (9′) Median lobe of males long: distance between ventral angular bend and apex, in lateral view, 4.6 to 5.3 mm; apex, in lateral view, wide (Fig. 66b), and in ventral view, thin-edged (10 microns) and twisted (Fig. 66a). From southern Oregon, southern Idaho, southwestern Montana and southward ..... *E. finitimus* Casey p. 303

10′ Median lobe of males short: distance between ventral angular bend and apex, in lateral view, 3.5 to 4.7 mm; apex in lateral view, wide (south of central British Columbia and southwestern Alberta) or narrow, and, in ventral view, thick-edged (35 microns), slightly twisted (south of central British Columbia and southwestern Alberta) or straight (Figs. 67a, 68a and 69a). North of central Oregon, central Idaho and Colorado, and east of these regions in forested areas ..... *E. americanus* Dejean p. 307

11 (5) Hind femur, in dorsal view, with three to seven long (about 150 microns) white setae subapically (Fig. 35). Apex of median lobe of males truncated (Fig. 63b). Specimen from northeastern China or Japan ..... *E. comatus* new species p. 311

11′ Hind femur, in dorsal view, with one to three small (40 to 80 microns) white setae subapically (Fig. 34). Apex of median lobe rounded (Fig. 61a) 12

12 (11′) Abdominal sternum 3 with less than 40 punctures laterally (Fig. 142). Punctures in pits separated by two to four rows of meshes of microsculpture (Fig. 136) 14

12′ Abdominal sternum 3 with 40 to 80 punctures laterally (Fig. 141). Punctures in pits separated by one to three rows of meshes of microsculpture 13

13 (12′) Microsculpture scale-like (best seen with diffused light) on abdominal sterna between ambulatory setae and edge of sternum (Figs. 143 and 153). Antennomere 3 without accessory seta. Elytron with one row of sharply delineated mirrors in most specimens (Fig.117). Tibia of foreleg mostly red-brown except for metallic apex and base. Boreal and temperate Palaearctic Region ..... *E. riparius* (Linnaeus) p. 313

13′ Microsculpture on abdominal sterna flat or subconvex--scale-like in some specimens of *E. tuberculatus* (Fig. 144). Antennomere 3, in most specimens, with some accessory setae. Elytron with two or three rows of sharply delineated mirrors in most specimens (Fig. 116). Tibia of foreleg of most specimens mostly or entirely metallic. Arctic and subarctic regions of Palaearctic and western Nearctic Regions ..... *E. tuberculatus* Mäklin p. 316

14 (12) Punctures 20 microns in diameter on elytral pits, and 25 microns on pronotum. Pronotum with long sinuation along lateral margin. Specimen from eastern Tibet, China ..... *E. tibetanus* Semenov p. 320

14′ Punctures of elytral pits and pronotum 25 to 30 microns in diameter. Pronotum with short sinuation along lateral margin. Tundra regions of western Nearctic Region and Commander Islands, U.S.S.R. ..... *E. parviceps* Van Dyke p. 319

First Instar Larvae

1 Antero-dorsal seta of abdominal epipleura 2 to 5 and 8 sub-equal and very small. Epicranial suture 0.2 to 0.3 as long as antennomere 1. Apical inner margin of mandible smooth, posterior margin of retinaculum toothed. Nearctic Region ..... *E. californicus* Mannerheim p. 299

1′ Antero-dorsal seta of abdominal epipleura 2 to 5 small and much larger than that of epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1. Apical inner margin of mandible toothed, if smooth, then posterior margin of retinaculum also smooth 2

2 (1′) Seta PII-P of nota about 20 microns in length, only slightly larger than that of terga. Seta VEM-P on parietale very small. Prairie regions of Nearctic Region ..... *E. lecontei* Crotch p. 295

2′ Seta PII-P of nota about 40 microns in length, abouth twice as long as that of terga. Seta VEM-P of parietale small ... 3

3 (2′) Antero-dorsal seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region ... *E. ruscarius* Say p. 293

3′ Antero-dorsal seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 ... 4

4 (3′) Apical inner margin of mandible and posterior margin of retinaculum smooth. Temperate or boreal Palaearctic Region ... *E. riparius* (Linnaeus) p. 313

4′ Apical inner margin of mandible and posterior margin of retinaculum clearly toothed ... 5

5 (4′) Seta AIM much smaller on tergum 8 than that of terga 1 to 5. Nearctic Region ... *E. americanus* Dejean p. 307

5′ Seta AIM as large on tergum 8 as that of terga 1 to 5. Western Nearctic Region ... *E. tuberculatus* Mäklin p. 316

Second Instar Larvae

1 Antero-dorsal basic seta of abdominal epipleura 2 to 5 and 8 subequal and very small. Epicranial suture less than 0.3 as long as antennomere 1. Nearctic Region ... *E. californicus* Mannerheim p. 299

1′ Antero-dorsal basic seta of abdominal epipleura 2 to 5 small yet much larger than same seta on epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1 ... 2

2 (1′) Seta PII-P of nota 10 to 20 microns in length, and subequal to that of terga. Seta VEM-P of parietale very small in most specimens. Prairie region of Nearctic Region ... *E. lecontei* Crotch p. 295

2′ Seta PII-P of nota moderately 40 to 60 microns in length, about twice as long as that of terga. Seta VEM-P of parietale small ... 3

3 (2′) Antero-dorsal basic seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region ... *E. ruscarius* Say p. 293

3′ Antero-dorsal basic seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 ... 4

4 (3′) Tergum 9 with dark brown urogomphus. Seta AII and AIM of nota small. Temperate or boreal Palaearctic Region ... *E. riparius* (Linnaeus) p. 313

4′ Tergum 9 with straw colored urogomphus. Seta AII and AIM of nota medium-sized to large ... 5

5 (4′) Seta AIM as large on tergum 8 as that of tergum 1 to 5. Northwestern Nearctic Region ... *E. tuberculatus* Mäklin p. 316

5′ Seta AIM much smaller on tergum 8 than that of terga 1 to 5. Nearctic Region ... *E. americanus* Dejean p. 307

Third Instar Larvae

1 Antero-dorsal basic seta of abdominal epipleura 2 to 5 and 8 subequal and very small. Epicranial suture less than 0.3 as long as antennomere 1. Nearctic Region ..... *E. californicus* Mannerheim p. 299

1′ Antero-dorsal basic seta of abdominal epipleura 2 to 5 small yet larger than that of epipleuron 8. Epicranial suture 0.3 to 0.6 as long as antennomere 1 2

2 (1′) Parietale much paler at base than elsewhere; pronotum pale in lateral 0.3. Seta PII-P of nota 10 to 20 microns in length, subequal to that on terga. Prairie region of Nearctic Region ..... *E. lecontei* Crotch p. 295

2′ Parietale dark or as pale as behind eyes; pronotum dark brown. Seta PII-P of nota 40 to 80 microns in length, and about twice as long as that of terga 3

3 (2′) Antero-dorsal basic seta of abdominal epipleuron 1 much smaller than that of epipleura 3 to 5. Temperate eastern Nearctic Region ..... *E. ruscarius* Say p. 293

3′ Antero-dorsal basic seta of abdominal epipleuron 1 as large as that of epipleura 3 to 5 4

4 (3′) Tergum 9 with dark brown urogomphus. Seta AII and AIM of nota small. Temperate or boreal Palaearctic Region .... *E. riparius* (Linnaeus) p. 313

4′ Tergum 9 with straw colored urogomphus. Seta AII and AIM of nota medium-sized to large 5

5 (4′) Seta AIM as large on tergum 8 as that of terga 1 to 5. Northwestern Nearctic Region ..... *E. tuberculatus* Mäklin p. 316

5′ Seta AIM much smaller on tergum 8 than that of terga 1 to 5 6

6 (5′) Pointed microsculpture absent from anterior and present laterally on 50% of posterior bands of terga 2 to 8. Western Nearctic Region ..... *E. finitimus* Casey p. 303

6′ Pointed microsculpture present on entire anterior and posterior bands of terga 2 to 8. Forested regions of Nearctic ... *E. americanus* Dejean p. 307

Elaphrus marginicollis new species
Figs. 20, 168

Elaphrus marginicollis new species. Type material: Holotype male and allotype female labelled: Jack's Gulch, Roosevelt N.F., COLORADO, July 25, 1970, Coll. R. Bell; type in United States National Museum of Natural History, Washington, D.C. Additional paratypes from this and other localities mentioned below.

Adults

Diagnostic combination.— Distinguished from adults of all other species of the subgenus by completely beaded lateral margin of pronotum, and by large punctures (40 to 50 microns) on pronotum and small punctures (25 microns) in elytral pits.

Description.— *Two color forms.* For details see color description under *E. lecontei* (p. 295) except the following. Tibiae black with metallic reflections over dorsal surface.

Antennomere 3 with few accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin moderately convex, beaded completely (Fig. 20), and not explanate before sinuation; disc with one pair of submedial impressions and without acessory setae. Metepisternum without accessory setae. Abdominal sterna of males and females with numerous accessory setae spread between ambulatory setae and lateral punctate area. Main mirror of elytron rectangular; mirrors sharply outlined, convex in three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite

Table 19. Descriptive statistics for *E. marginicollis*, based on six males and six females from Colorado, Wyoming, Washington and California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.70–2.00	1.90	0.132	0.051	4.6
PW	1.85–2.22	2.06	0.159	0.061	5.1
EL	4.30–5.00	4.64	0.353	0.136	5.1
EW	1.60–1.95	1.73	0.166	0.064	6.4
HW	2.00–2.22	2.12	0.127	0.049	4.0
B. Proportions					
PL/PW	0.876–0.962	0.922	0.034	0.014	2.5
PL/EL	0.370–0.443	0.410	0.027	0.010	4.4
PL/EW	1.026–1.154	1.099	0.061	0.024	3.7
PL/HW	0.850–0.930	0.893	0.039	0.014	2.9
PW/EL	0.402–0.477	0.445	0.030	0.012	4.5
PW/EW	1.128–1.242	1.193	0.057	0.022	3.2
PW/HW	0.925–1.000	0.969	0.033	0.012	2.3
EL/EW	2.559–2.875	2.683	0.156	0.060	3.9
EL/HW	2.000–2.326	2.182	0.139	0.054	4.3
EW/HW	0.776–0.867	0.813	0.042	0.016	3.4

straight) and slightly impressed (Figs. 116, 128). Dorso-subapical surface of hind femur with one to three short setae (Fig. 34).

Integument sculpture. Punctures 25 to 30 microns in diameter on head and elytra, and 40 to 50 microns in diameter on pronotum and abdomen. Punctures 20 microns apart submedially and 35 microns apart antero-laterally on pronotum, 10 microns apart in elytral pits, and 25 microns apart on elytral intervals 4, 6 and 8. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture on head, pronotum, elytral intervals, thoracic pleura and abdominal sterna (between ambulatory setae and lateral punctate area) subconvex.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61). Parameres with short setae (Fig. 62b).

Measurements and proportions.— One sample studied. See Table 19.

Derivation of specific epithet.— From latin *marginalis* meaning margined and *collum* meaning neck, referring to completely beaded and margined lateral edge of pronotum.

Distribution.— Known from the Rocky and Siskiyou Mountains (Fig. 168).

United States. - COLORADO: Kenosha Pass (1;AMNH); Jack's Gulch, Roosevelt N.F. (8;USNM, UVCC). WYOMING: Laramie (1:USNM). WASHINGTON: Pullman (1;WSUC). CALIFORNIA: Siskiyou Co. (1;CASC).

Collecting notes.— At Jack's Gulch, Colorado, R.T. Bell found adults along a small spring in a sunny area on moderately firm, organic and wet soil.

Taxonomic notes.— I studied 12 specimens and dissected three males.

Geographical affinities.— The range of this species overlaps those of *E. californicus, E. americanus, E. finitimus* and *E. lecontei.*

Elaphrus lheritieri Antoine
Figs. 23, 64a-b, 77a, 105, 115, 127, 168

Elaphrus lheritieri Antoine, 1947:26. Type locality: 35 km from Safi port between Tleta bou Guedra and Djama Sahim, Morocco; type not seen. Antoine, 1955:47. Jeanne, 1966:16.

Adults

Diagnostic combination.— Distinguished from adults of all other species by immense elytral pits, and very sinuate or almost unrecognizable intervals 4, 6 and 8.

Description.— Only green specimens seen. For details see color under green form of *E. lecontei* (p. 295). Abdominal sterna brilliant green.

Antennomere 3 without accessory setae. Frons with clearly outlined foveola, and without accessory setae. Pronotum with lateral margin convex, obsolete and not beaded in sinuation, and clearly explanate before sinuation (Figs. 23, 77a, 105); disc with two pairs of submedial impressions, and with numerous accessory setae. Abdominal sterna of both sexes with moderate number of accessory setae between ambulatory setae. Main mirror of elytron oval; only main mirror sharply outlined and convex (Fig. 127). Elytral pits immense (intervals 4, 6 and 8 narrow and sinuated between pits), and very deeply impressed (Figs. 115, 127). Dorso-subapical surface of hind femur with one to three short (about 60 microns) setae (Fig. 34).

Integument sculpture. Punctures 25 microns in diameter dorsally, and 35 microns in diameter ventrally. Punctures 10 to 20 microns apart on pronotum, 5 to 10 microns apart in elytral pits, and 10 to 15 microns apart on intervals 4, 6 and 8. First sutural pit of elytron with six or seven concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture subconvex dorsally, convex on thoracic pleura, and flat with weakly outlined meshes on abdominal sterna (surface brilliant).

Male genitalia. Apex of median lobe in ventral thin-edged and slightly twisted, and in lateral view axe-shaped (Figs. 64a, 64b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61). Setae of parameres long (Fig. 69c).

Measurements and proportions.— Based on six specimens from Abda and Safi, Morocco. PL, 1.50-1.66-1.70 mm; PW, 1.90-2.07-2.20 mm; EL, 3.80-4.12-4.30 mm; EW, 1.50-1.70-1.80 mm; HW, 1.80-1.92-2.10 mm; PL/PW, 0.756-0.800-0.821; PL/EL, 0.835-0.402-0.414; PL/EW, 0.980-0.976-1.000; PL/HW, 0.819-0.842-0.853; PW/EL. 0.477-0.503-0.542; PW/EW, 1.137-1.221-1.286; PW/HW. 1.025-1.052-1.084; EL/EW. 2.371-2.427-2.478; EL/HW. 1.025-1.052-1.084; EL/EW, 2.371-2.427-2.478; EL/HW, 2.000-2.094-2.175; EW/HW, 0.837-0.863-0.912.

Distribution.— Known from Morocco and northern Spain (Jeanne, 1966).

Morocco. -ABDA; (2;CJea), Safi (3;CJea, HGou), 35 km e. Safi between Tatla bou Guedra and Djama Sahim (type locality Antoine, 1955), Foucould (Antoine, 1955). Spain. - PALENCIA: Carrion de los Condes (Antoine, 1955, and Jeanne, 1966).

Collecting notes.— Antoine (1947) collected adults on clay beaches of small temporary pools, "dayas", in mid-April after the winter rainy season. Adults were running during hot sunny weather between grasses on wet and dry mud. Apparently adults are not found by more permanent pools. Jeanne (1966) described the habitat as pools associated with saline soil.

Taxonomic notes.— This species is readily recognized from the original description.

I studied six specimens, and dissected one male.

Geographical affinities.— The range of this species does not overlap with those of other species.

Elaphrus mimus new species
Figs. 21, 77a, 168

Elaphrus mimus new species. - Type material: Holotype male and allotype female labelled: Angwin, Cal., 5 (May) - 16 - 57, B. Cox; type in California Academy of Sciences, San Francisco.

Adults

Diagnostic combination.— Distinguished by following combination: Punctures of pronotum as dense submedially as laterally (25 microns apart); pronotum and head with numerous and widespread accessory setae; two false pits present near main mirror in interval 4.

Description.— Two color forms. For details see under *E. lecontei* (p. 295) except the following. Intervals 4 and 6 with two false pits outlined in purple.

Antennomere 3 with few accessory setae. Frons without impression medially, and with numerous accessory setae. Pronotum with lateral margin convex, obsolete and not beaded in sinuation, and slightly explanate before sinuation (Fig. 77b); disc without submedial impressions, and with numerous and widespread accessory setae. Metepisternum with some accessory setae. Abdominal sterna of both sexes with numerous accessory setae extended between ambulatory setae and lateral punctate area. Main mirror on elytron oval; main mirror sharply outlined, others absent or suggested. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight), and slightly impressed (Figs. 116, 128). Dorso-subapical surface of hind femur with one to three short setae (Fig. 34).

Integument sculpture. Punctures 25 microns in diameter on dorsal surface, and 30 to 35 microns in diameter on ventral surface. Punctures 20 to 25 microns apart on pronotum, 1 to 5 microns apart in elytral pits, and 5 to 10 microns apart on most of intervals 4, 6 and 8. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 30 to 50 punctures on each side.

Microsculpture absent or meshes weakly outlined in spots on dorsal body surface, subconvex ventrally, and flat without points on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 62b). Parameres with short setae (Fig. 62b).

Measurements and proportions.— Based on two specimens from Anguin, California. PL, 1.6-1.7 mm; PW, 1.9-2.0 mm; EL, 4.1-4.2 mm; EW, 1.6-1.7 mm; HW, 1.9-2.0 mm; PL/PW, 0.82-0.87; PL/EL, 0.38-0.42; PL/EW, 0.95-1.09; PL/HW, 0.83-0.90; PW/EL, 0.46-0.48; PW/EW, 1.16-1.25; PW/HW, 1.01-1.03; EL/EW, 2.54-2.59; EL/HW, 2.13-2.21; EW/HW, 0.82-0.87.

Derivation of specific epithet.— From Latin *mimus* meaning mime or actor, referring to its apparent similarity in dorsal view with *E. finitimus* of California.

Distribution.— Known only from the type locality and presumed to be in the hills north of this locality (Fig. 168).

Collecting notes.— Found on sun exposed clay beaches of a small lake.

Taxonomic notes.— I studied two specimens and dissected one male.

Geographical affinities.— The range of this species overlaps those of *E. californicus, E. finitimus* and perhaps also that of *E. viridis.*

Elaphrus viridis Horn
Figs. 22, 77c, 106, 114, 126, 168

Elaphrus viridis Horn, 1878:52. Type locality: California; type (not seen) in Museum of Comparative Zoology, Cambridge, Massachusetts. Schaupp, 1878:6. Austin, 1880:5. Bänninger, 1931:184. Lindroth, 1961:110.

Elaphrus horni Csiki, 1927:420. New name for *E. viridis* Horn, a junior homonym of *E. riparius* var. *viridis* Letzner, 1849:52. Lindroth (1961) rejected Csiki's name as invalid since Letzner clearly referred to a color variation of *E. riparius.* Bänninger, 1931:184. Lindroth, 1961:110.

Adults

Diagnostic combination.— Distinguished from adults of other species by its magnificent and brilliant green color, and lack of outlined pits on elytra.

Description.— Two forms: multi-mirrors and single-mirror (along lateral margin near sinuation). In both forms: dorsal body surface bright green, except for bright copper patterns on head and pronotum and dark copper intervals 3, 5 and 7 between mirrors (same intervals bright green in single-mirror form). Ventral surface brilliant green, but abdominal sternum 6 brownish. Tibiae brown, but metallic at base and apex.

Table 20. Descriptive statistics for *E. viridis*, based on four males and six females from California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.22–1.47	1.36	0.097	0.041	4.8
PW	1.72–2.00	1.84	0.137	0.068	5.0
EL	3.55–4.05	3.74	0.276	0.116	4.9
EW	1.32–1.60	1.46	0.135	0.057	6.1
HW	1.67–1.80	1.73	0.068	0.029	2.6
B. Proportions					
PL/PW	0.689–0.775	0.741	0.042	0.018	3.8
PL/EL	0.349–0.387	0.364	0.017	0.006	3.0
PL/EW	0.879–1.038	0.930	0.072	0.030	5.2
PL/HW	0.750–0.819	0.785	0.036	0.014	3.0
PW/EL	0.475–0.507	0.491	0.017	0.008	2.2
PW/EW	1.217–1.340	1.256	0.057	0.024	3.0
PW/HW	1.015–1.127	1.060	0.052	0.022	3.3
EL/EW	2.500–2.679	2.555	0.088	0.038	2.3
EL/HW	2.058–2.250	2.158	0.091	0.038	2.8
EW/HW	0.779–0.889	0.845	0.054	0.022	4.3

Antennomere 3 with some accessory setae. Frons without medial impressions, but with numerous long accessory setae. Pronotum with lateral margin convex, unbeaded and obsolete in sinuation, and explanate before sinuation, (Figs. 22, 77c, 106); disc without submedial impressions, and with numerous long accessory setae. Metepisternum with accessory setae. Abdominal sterna of both sexes with numerous accessory setae extended to edge of sternum 5. Main mirror of elytron roughly oval; mirrors sharply outlined in three rows (Fig. 126), or only one mirror along lateral margin near sinuation. Elytral pits not impressed or outlined (Figs. 114, 126). Dorso-subapical surface of hind femur with many long setae (Fig. 35).

Integument sculpture. Punctures 25 microns in diameter on dorsal and ventral surface, and 15 to 25 microns in diameter on bright copper surfaces. Punctures two to five microns apart on dorsal surface, 10 to 15 microns apart on bright copper surfaces, and 25 microns apart ventrally. Number of concentric rows of punctures around setigerous punctures of elytron difficult to estimate, thus not given here. Third visible abdominal sternum with 40 to 60 punctures on each side.

Microsculpture absent dorsally, and subconvex or flat on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 62b). Setae of parameres long (Fig. 69c).

Measurements and proportions.— One sample studied, see Table 20.

Distribution.— Known from California, and rediscovered in 1967 south of Sacramento, California in the Central Valley (Fig. 168).

United States. - CALIFORNIA (9;ANSP, MCZC, CASC, INHS), Solano Co., 9.5 mi. s. Dixon (3;CASC, CNCI, UASM), Solano Co., 10 mi. s. Dixon (1;UCDC).

Collecting notes.— Near Dixon a few specimens were found between *Juncus* on fine clay mud. Adults were inactive in early May. The small pool was mostly dry at the start of the dry season. Kavanaugh (pers. comm.) feels that this habitat may be a refuge area at the start of the dry season, and that their true habitat would probably be flooded grassland. *E. viridis* is regarded as an endangered species, and permits must be sought to collect specimens.

Taxonomic notes.— The adults of this species were recognized from the original description.

I studied 13 adults, and dissected two males.

Geographical affinities.— The range of this species overlaps those of *E. californicus, E. finitimus* and perhaps also that of *E. mimus.*

Elaphrus hypocrita Semenov
Fig. 62a-b

Elaphrus hypocrita Semenov, 1926:39. Type area: Russian Turkestan; type not seen.
Elaphrus smaragdiceps; Bänninger, 1919:148 (*nec* Semenov, 1889). Semenov, 1926:39.

Adults

Diagnostic combination.— Among Palaeartic species, adults are easily recognized by restricted distribution of accessory setae on abdominal sterna (not extended to lateral edge), by short setae on parameres, and by brilliant abdominal sterna (excluding *E. comatus*). In relation to all species, adults of this species are best characterized by character combination in key.

Description.— Two color forms. For details see under *E. lecontei* (p. 295) except the following. Intervals 4 and 6 without false pits outlined in purple.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, unbeaded and suggested in sinuation, and not explanate in front of sinuation (Figs. 25, 77d); disc with one pair of impressions submedially and without accessory setae. Metepisternum without accessory setae. Abdominal sterna in males and females with scattered accessory setae between ambulatory setae. Main mirror of elytron rectangular; main mirror sharply outlined, others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight), and slightly impressed (Fig. 116). Dorso-subapical surface of hind femur with one or two short (40 to 50 microns) setae (Fig. 34).

Integument sculpture. Punctures 20 to 25 microns in diameter dorsally, and 30 to 35 microns in diameter ventrally. Punctures 15 to 25 microns apart medially and 30 to 40 microns apart antero-laterally on pronotum, 5 to 10 microns apart in elytral pits, 10 to 20 microns apart on elytral intervals 4, 6 and 8, and 30 microns apart on proepisternum. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 40 to 60 punctures on each side.

Microsculpture convex or subconvex on most of dorsal body surface and thoracic pleura, and flat on abdominal sterna especially between ambulatory setae and lateral margin, surface brilliant.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 62a, 62b); base of lobe along ventral angular bend narrowly sclerotized with ventral membrane visible in lateral view (Fig. 61). Setae of parameres short (Fib. 62b).

Measurements and proportions.— Based on six specimens from Wernyi (old Turkestan). PL, 1.5-1.67-1.7 mm; PW, 1.6-1.80-1.9 mm; EL, 3.9-4.16-4.3 mm; EW, 1.5-1.59-1.6 mm; HW, 1.7-1.91-2.0 mm; PL/PW, 0.917-0.924-0.932; PL/EL, 0.385-0.400-0.407; PL/EW, 1.000-1.049-1.079; PL/HW, 0.835-0.873-0.893; PW/EL, 0.417-0.433-0.442; PW/EW, 1.083-1.136-1.161; PW/HW, 0.911-0.945-0.974; EL/EW, 2.585-2.622-2.667; EL/HW, 2.063-2.183-2.234; EW/HW, 0.785-0.832-0.857.

Distribution.— Known from the north shore of the Black Sea to western China (Semenov, 1926).

Taxonomic notes.— I studies six adults and dissected two males.

Geographical affinities.— The range of this species overlaps that of E. riparius.

Elaphrus ruscarius Say
Figs. 60a-b, 109, 168

Elaphrus ruscarius Say, 1834:417. Type locality: Pennsylvania subsequently designated by Lindroth (1961); Lindroth and Freitag (1969) designated a male from Columbia, Penn. as neotype; the neotype is in the LeConte Collection in the Museum of Comparative Zoology, Cambridge, Massachusetts. Say, 1823:496. 1834:529. LeConte,

Table 21. Descriptive statistics for *E. ruscarius*, based on ten males and nine females from Vermont.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.54	0.094	0.029	4.1
PW	1.50–1.87	1.68	0.149	0.046	5.9
EL	3.40–4.15	3.82	0.294	0.090	5.1
EW	1.40–1.65	1.53	0.115	0.035	5.0
HW	1.70–2.00	1.86	0.110	0.034	3.9
B. Proportions					
PL/PW	0.836–1.048	0.919	0.069	0.022	5.0
PL/EL	0.375–0.441	0.402	0.024	0.008	4.0
PL/EW	0.955–1.053	1.008	0.040	0.012	2.7
PL/HW	0.773–0.880	0.827	0.039	0.012	3.1
PW/EL	0.414–0.467	0.438	0.024	0.004	3.6
PW/EW	1.000–1.197	1.099	0.066	0.020	4.0
PW/HW	0.840–0.945	0.901	0.048	0.014	3.5
EL/EW	2.386–2.667	2.506	0.102	0.032	2.7
EL/HW	1.947–2.192	2.057	0.109	0.034	3.5
EW/HW	0.760–0.868	0.821	0.043	0.014	3.5

1853:401. Crotch, 1873:4. Mäklin, 1877:17. Schaupp, 1878:6. Blatchley, 1910:48 *(ex parte)*. Bänninger, 1919:148. Hatch, 1953:63. Lindroth, 1961:119. Lindroth and Freitag, 1969:332.

Elaphrus americanus; LeConte, 1853:402. Mäklin, 1877:17. *nec* Dejean, 1831.

Elaphrus texanus Casey, 1924:17. Type locality: Galveston, Texas; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:119.

Adults

Diagnostic combination.— Distinguished from adults of other species by apparently large proepisternal punctures (60 microns). In reality punctures 30 to 40 microns, but appearing larger since areas around them are depressed.

Description.— Two color forms. For details see under *E. lecontei* (p. 295) except following. Ventral punctures blue-green; smooth and microsculptured surface of thoracic pleura dark copper (almost black on propleuron), and green elsewhere.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obsolete and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and without accessory setae. Abdominal sterna of both sexes with numerous accessory setae between ambulatory setae and lateral punctate area. Main mirror of elytron rectangular; one to three subsutural mirrors sharply outlined, others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and moderately impressed. Dorso-subapical surface of hind femur with one or two short (40 to 60 microns) setae (Fig. 34).

Integument sculpture. Punctures 25 to 30 microns in diameter on most of head, pronotum and elytra, and 30 to 40 microns in diameter on elytral pits, abdominal sterna and thoracic pleura. Punctures 20 microns apart on elytral intervals 4, 6 and 8, submedially on pronotum and on head, 5 to 15 microns apart in elytral pits, 35 microns apart on thoracic pleura, on abdominal sterna, and antero-laterally on pronotum. First sutural pit of elytron with three to four concentric rows of punctures. Third visible abdominal sternum with 30 to 40 punctures on each side.

Microsculpture convex or subconvex over most of dorsal body surface and thoracic pleura, and flat and without points on abdominal sterna between ambulatory setae and lateral punctate area.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 60a, 60b); base of lobe along ventral angular bend widely sclerotized, and ventral membrane not visible in lateral view. Setae of parameres long (Fig. 69c).

Measurements and proportions.— Five samples studied, and data for one presented in Table 21.

Variation.— Between northern and southern samples no obvious differences were observed. Copper coloured individuals are known to me only from regions with red soils. This color form is probably cryptic on these soils.

All Instar Larvae

Diagnostic combination.— Recognized from larvae of other species by combination of characters in key.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much larger than that on terga. Seta AIM on terga abruptly short, at least on tergum 8. Antero-dorsal seta of abdominal epipleura 1 and 8 very small, and markedly larger on epipleura 2 to 7.

Second and Third Instar Larvae

Description.— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

Geographical Distribution and Affinities, and Notes

Distribution.— Restricted to eastern North America, from the Atlantic coast to the prairies, and from northern Minnesota and southern Maine in the north, to southern Georgia, Louisiana and eastern Texas in the south (Fig. 168).

Collecting notes.— Found on many types of wet beaches (clay, sand, silt and organic) in swamps, along small rivers and ditches. The substrate is usually free of vegetation and sun-exposed.

Taxonomic notes.— Casey's holotype (*E. texanus*) represents a typical adult of this species.

I studied more than 4000 adults, and dissected six males. I examined two first, one second and on third instar larvae from northern Arkansas.

Geographical affinities.— The range of this species overlaps those of *E. californicus, E. americanus* (marginally) and *E. lecontei* (marginally).

Elaphrus lecontei Crotch.
Figs. 13, 24, 65a-b, 75, 81, 91a-b, 130, 169

Elaphrus lecontei Crotch, 1876:246. Type locality: Longs Peak, Colorado; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. Crotch, 1873:6. Schaupp, 1878:6. La Rivers, 1946:138. Hatch, 1953:63. Lindroth, 1961:114.

Elaphrus intermedius LeConte, 1848;448 (*nec* Kirby, 1837). Crotch, 1873:6. 1876:246. Schaupp, 1878:6. Lindroth, 1961:114.

Elaphrus devinctus Casey, 1920:139. Type locality: Wray, Colorado; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington D.C. Lindroth, 1961:114.

Elaphrus spissicornis Casey, 1924:18. Type locality: Parowan, Utah; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:114.

Table 22. Descriptive statistics for *E. lecontei*, based on ten males and nine females from Manitoba.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.62–1.95	1.79	0.133	0.041	4.9
PW	2.00–2.32	2.16	0.144	0.044	4.4
EL	4.10–4.85	4.45	0.349	0.107	5.2
EW	1.57–1.90	1.75	0.138	0.042	5.3
HW	2.00–2.27	2.11	0.121	0.037	3.8
B. Proportions					
PL/PW	0.772–0.878	0.831	0.040	0.012	3.2
PL/EL	0.374–0.431	0.399	0.021	0.006	3.5
PL/EW	0.956–1.108	1.026	0.066	0.020	4.3
PL/HW	0.802–0.889	0.852	0.037	0.012	2.9
PW/EL	0.454–0.506	0.481	0.019	0.006	2.7
PW/EW	1.178–1.299	1.234	0.057	0.018	3.1
PW/HW	0.976–1.095	1.026	0.046	0.014	3.0
EL/EW	2.429–2.716	2.568	0.102	0.032	2.6
EL/HW	2.000–2.259	2.136	0.111	0.034	3.5
EW/HW	0.782–0.881	0.832	0.043	0.014	3.5

Adults

Diagnostic combination.— Distinguished from adults of other species by wider pronotum with sharply delineated anterior transverse stria toward anterior angle (Fig. 24), by dense pubescence on antennomere 3, and by six to ten rows of puncture in first sutural pit of elytron.

Description.— Two color forms. Green form: microsculptured and smooth surfaces dark copper on most of elytra, on portions of pronotum and head, bright copper on portions of pronotum and head, and purple near center of elytral pits; punctures green but purple near center of elytral pits. Ventral punctures green; smooth and microsculptured surfaces dark copper on pleura and green on abdominal sterna. Copper form: as above but punctures copper dorsally. In both forms: interval 4 with purple false pit near main mirror in many specimens; tibia red-brown and metallic at base and apex.

Antennomere 3 setose in apical 0.5, especially along posterior side (Fig. 13). Frons without medial impression and accessory setae. Pronotum with lateral margin convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 24, 77d); disc with one or two pairs of submedial impressions, without accessory setae, with sharply defined antero-transverse stria toward anterior angle, and generally with mirrors near main submedial impression (Fig. 24). Abdominal sterna with sparse setae between ambulatory setae; setae more numerous in males than in females. Main mirror of elytron rectangular; mirrors sharply outlined on intervals 3, 3 and 5, or 3, 5 and 7; mirrors absent or developed in elytral pits. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly to deeply impressed (Fig. 130). Dorso-subapical surface of hind femur with one to three short (40 to 60 microns) setae (Fig. 34).

Integument sculpture. Punctures 20 to 25 microns in diameter on dorsal body surface, 25 to 30 microns in diameter on abdominal sterna, and 30 to 35 microns in diameter on thoracic pleura. Punctures 2 to 5 microns apart in elytral pits, 2 to 15 microns apart on elytral intervals, submedially on pronotum, and on head, 20 to 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit with six to ten concentric rows of punctures. Abdominal sternum 3 with 70 to 100 punctures on each side.

Microsculpture of dorsal body surface generally absent or meshes weakly outlined, but in spots subconvex or convex on thoracic pleura, and flat or subconvex on abdominal sterna between ambulatory setae and lateral punctate portion.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view wide and long (Figs. 65a, 65b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres long (Fig. 69c).

Table 23. Descriptive statistics for *E. lecontei*, based on ten males and ten females from Lower Klamath Lake, Oregon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.67–1.95	1.85	0.116	0.035	4.2
PW	2.00–2.40	2.21	0.148	0.044	4.5
EL	4.35–5.40	4.84	0.412	0.123	5.7
EW	1.67–2.02	1.83	0.150	0.045	5.4
HW	2.00–2.27	2.15	0.120	0.036	3.7
B. Proportions					
PL/PW	0.774–0.905	0.836	0.046	0.014	3.7
PL/EL	0.349–0.442	0.382	0.028	0.008	5.0
PL/EW	0.905–1.087	1.008	0.072	0.022	4.8
PL/HW	0.807–0.905	0.859	0.040	0.012	3.1
PW/EL	0.432–0.484	0.457	0.021	0.006	3.1
PW/EW	1.122–1.294	1.206	0.063	0.018	3.5
PW/HW	1.000–1.060	1.027	0.030	0.008	1.9
EL/EW	2.553–2.750	2.640	0.079	0.024	2.0
EL/HW	2.140–2.374	2.249	0.105	0.032	3.1
EW/HW	0.800–0.892	0.852	0.037	0.012	2.9

Measurements and proportions.— Fifteen samples studied, and data for three presented in Tables 22 to 24.

Variation.— Specimens from the San Luis Valley in southern Colorado are strikingly different from any other samples. In this area adults are characterized as follows: all elytral mirrors convex and sharply outlined; mirrors developed in elytral pits and near submedial impression of pronotum; punctures larger dorsally as shown by fewer rows of punctures in pit anterior to main mirror; elytra more convex (similar to adults of *E. californicus).* Remaining samples show more subtle differences and are discussed in a coming study on variation among populations.

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by very small seta VEM-P on parietale, and by subequal seta PII=P on nota and terga.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.3 to 0.5 as long as antennomere 1. Seta VEM-P of parietale very small. Seta PII-P of nota very small and subequal to that on terga. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleura markedly smaller than on segments 3 to 5.

Table 24. Descriptive statistics for *E. lecontei*, based on ten males and ten females from Lone Pine, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.85–2.15	2.03	0.104	0.031	3.4
PW	2.30–2.70	2.52	0.129	0.038	3.4
EL	4.70–5.50	5.12	0.298	0.089	3.9
EW	1.82–2.15	2.02	0.112	0.033	3.7
HW	2.22–2.55	2.39	0.103	0.031	2.9
B. Proportions					
PL/PW	0.769–0.835	0.807	0.021	0.006	1.7
PL/EL	0.377–0.426	0.398	0.019	0.006	3.3
PL/EW	0.965–1.025	1.009	0.046	0.014	3.1
PL/HW	0.814–0.887	0.851	0.028	0.008	2.2
PW/EL	0.468–0.510	0.493	0.021	0.006	2.8
PW/EW	1.198–1.299	1.250	0.045	0.014	2.4
PW/HW	1.031–1.103	1.055	0.027	0.016	1.7
EL/EW	2.447–2.625	2.537	0.075	0.022	2.0
EL/HW	2.040–2.245	2.142	0.079	0.026	2.8
EW/HW	0.808–0.878	0.844	0.028	0.008	2.3

Second Instar Larvae

Description.— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

Third Instar Larvae

Description.— Head paler at base than behind eyes, and pronotum pale in lateral 0.3.

Geographical Distribution and Affinities, and Notes

Distribution.— Known from grasslands of western North America where there are alkaline marshes or creeks, but isolated near Great Slave Lake and along James Bay(2;CSWC, CNCI) (Fig. 169).

Collecting notes.— Adults are found on sun-exposed alkaline beaches of lakes, marshes and creeks. In most of the range, adults occur only near slightly alkaline waters, but in California, Utah and Great Slave Lake, Northwest Territories, they are also found on deeply crusted alkaline beaches. Beaches are free of vegetation, and are in relatively sheltered areas (especially near lakes). Adults run even on water-saturated soil near water edge, and are found under small stones or in crevices when inactive. The soil of upper beaches, in some of the localities studied, is red, thus copper individuals, in spring time, would be cryptically colored.

Taxonomic notes.— The holotype of *E. divinctus* Casey matches specimens of *E. lecontei* east of the Rockies, while that of *E. spissicornis* Casey matches those west of the Rockies. The first mention of the specific epithet *lecontei* by Crotch (1873:6) was not valid as there was no description. Crotch (1873) very ambiguously referred to a specimen identified and keyed as *E. intermedius* by LeConte (1848:448).

Table 25. Descriptive statistics for *E. californicus*, based on ten males and ten females from Maryland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.50–1.75	1.59	0.108	0.032	4.5
PW	1.55–1.85	1.66	0.131	0.039	5.3
EL	3.25–3.87	3.55	0.252	0.075	4.7
EW	1.35–1.60	1.48	0.108	0.032	4.8
HW	1.75–2.00	1.90	0.108	0.032	3.8
B. Proportions					
PL/PW	0.863–1.015	0.961	0.055	0.016	3.8
PL/EL	0.426–0.465	0.450	0.016	0.004	2.4
PL/EW	0.984–1.155	1.077	0.057	0.016	3.5
PL/HW	0.772–0.875	0.839	0.042	0.012	3.3
PW/EL	0.441–0.493	0.469	0.021	0.006	3.0
PW/EW	1.083–1.185	1.121	0.043	0.012	2.6
PW/HW	0.838–0.925	0.874	0.039	0.012	3.0
EL/EW	2.295–2.552	2.393	0.105	0.032	2.9
EL/HW	1.757–1.959	1.865	0.084	0.024	3.0
EW/HW	0.753–0.810	0.780	0.024	0.008	2.1

I studied more than 1000 adults, and dissected ten males. I examined six first instar, five second instar and three third instar larvae from Miquelon Lakes Provincial Park, Alberta.

Geographical affinities..— The range of this species overlaps those of *E. californicus, E. finitimus, E. americanus.* In its extreme eastern limit its range overlaps that of *E. ruscarius.* The range of *E. marginicollis,* a high altitude species, is probably parapatric with that of *E. lecontei.*

Elaphrus californicus Mannerheim
Figs. 35, 77d, 140, 154, 155, 172

Elaphrus californicus Mannerheim, 1843:190. Type locality: California; lectotype, designated by Lindroth, in Zoological Museum, University of Helsinki, Finland. LeConte, 1853:402. Crotch, 1876:246. Schaupp, 1878:6. Lindroth, 1961:118.

Elaphrus similis LeConte, 1848:449. Type locality: Longs Peak, Colorado; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachussetts. LeConte, 1853:402. Schaupp, 1878:6. Lindroth, 1961:118.

Elaphrus intermedius; Walker, 1866:309 (*nec* Kirby, 1837).

Elaphrus riparius; Crotch, 1873:4 *(ex parte).* Schaupp, 1878:6 *(ex parte).* Taylor, 1886:35 *(ex parte).* Harrington, 1889:139 *(ex parte).* Venables, 1913:26 *(ex parte).* Hippisley, 1922:63 *(ex parte).* La Rivers, 1946:138 *(ex parte).* Clark 1948:25 *(ex parte).* Hatch, 1953:63 *(ex parte). nec* Linnaeus, 1758.

Elaphrus ruscarius; Blatchley, 1910:48 *(ex parte)* (*nec* Say, 1834).

Elaphrus hesperius Casey, 1920:138. Type locality: Humboldt Co., California; lectotype (seen by me) designated by Lindroth (1975:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:118.

Table 26. Descriptive statistics for *E. californicus*, based on ten males and ten females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.55	0.093	0.028	4.0
PW	1.52–1.77	1.63	0.114	0.035	4.8
EL	3.50–4.00	3.69	0.219	0.066	4.0
EW	1.40–1.60	1.49	0.091	0.027	4.1
HW	1.70–1.97	1.84	0.109	0.033	4.0
B. Proportions					
PL/PW	0.900–1.016	0.953	0.048	0.014	3.6
PL/EL	0.399–0.438	0.422	0.015	0.004	2.4
PL/EW	0.966–1.103	1.044	0.046	0.014	3.0
PL/HW	0.817–0.878	0.846	0.025	0.008	2.0
PW/EL	0.420–0.467	0.443	0.019	0.006	2.9
PW/EW	1.066–1.138	1.096	0.033	0.010	2.0
PW/HW	0.840–0.945	0.888	0.045	0.014	3.4
EL/EW	2.323–2.554	2.476	0.089	0.026	2.4
EL/HW	1.896–2.164	2.006	0.084	0.024	2.8
EW/HW	0.753–0.868	0.811	0.039	0.012	3.2

Adults

Diagnostic combination.— Distinguished from adults of other species by following character combination: dorso-apical setae on hind femur long; proepisternal punctures dense (10 to 20 microns apart); accessory setae on abdominal sterna sparse.

Description.— In most populations one color form: gray-green or almost black, but in other populations, with bicolored individuals. Gray-green form: microsculptured and smooth surfaces on dorsal surface brass to black, copper in spots on pronotum and head, and purple near center of pits; punctures blue-green but purple near center of pits. Ventral surface with green punctures; microsculptured and smooth surfaces red purple on proepisternum, brass on other pleura, and green on sterna. Bicolored form: head, pronotum and extreme base of elytra as for gray-green form: rest of elytra with microsculptured and smooth surfaces black or copper; punctures almost black or dark copper (elytra at low magnification appear black), or copper (elytra at low magnification appear red-purple); pits better outlined with large copper punctures in outer 0.3. Black form (southern Oregon and adjacent California): microsculptured and smooth areas brilliant black dorsally; punctures dark blue-green, and pits better outlined with large green punctures in outer 0.3 (dorsal surface, at low magnification, appear much darker as mirrors are mostly fused). In all forms, interval 4 of some specimens with purple false pit near main mirror; tibiae red-brown, but metallic at base and apex.

Antennomere 3 without accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin little convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and without accessory setae. Abdominal sterna with few scattered setae; setae more numerous in males than in females. Main mirror of elytron rectangular; main mirror well outlined, others suggested or absent, but in black form most mirrors well outlined and fused with others. Elytral pits moderately wide (interval 4,6 and 8 quite straight) and generally quite impressed. Dorso-subapical surface of hind femur with five to ten long (80 to 150 microns) setae (Fig. 35).

Integument sculpture. Punctures 20 to 25 microns in diameter dorsally (generally 15 to 20 microns in prairie region), 30 microns in diameter along outer margin of pits, and 35 to 40 microns in diameter on abdominal sterna and thoracic pleura. Punctures 2 to 5 microns apart in elytral pits, 10 to 15 microns apart on elytral intervals (but 10 to 30 microns apart in black form), 5 to 10 microns apart medially and 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit of elytron with four to six concentric rows of punctures. Third visible

Table 27. Descriptive statistics for *E. californicus*, based on ten males and ten females from Seattle, Washington.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.87	1.73	0.114	0.034	4.4
PW	1.67–1.92	1.88	0.100	0.030	3.8
EL	3.50–4.25	3.93	0.283	0.084	4.8
EW	1.40–1.62	1.56	0.100	0.030	4.3
HW	1.75–2.07	1.92	0.108	0.035	4.1
B. Proportions					
PL/PW	0.905–1.014	0.959	0.043	0.012	3.0
PL/EL	0.404–0.463	0.441	0.024	0.008	3.6
PL/EW	1.047–1.175	1.110	0.051	0.016	3.1
PL/HW	0.873–0.948	0.902	0.033	0.010	2.4
PW/EL	0.432–0.487	0.461	0.024	0.008	3.5
PW/EW	1.092–1.224	1.158	0.050	0.014	2.8
PW/HW	0.875–0.987	0.941	0.042	0.012	3.0
EL/EW	2.413–2.596	2.516	0.085	0.026	2.3
EL/HW	1.900–2.184	2.046	0.114	0.034	3.7
EW/HW	0.771–0.855	0.813	0.037	0.012	3.1

abdominal sternum with 150 to 200 punctures on each side. Microsculpture generally convex dorsally (generally absent in black form) and ventrally on thoracic pleura, and subconvex on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view spatulate (Figs. 61a and 61b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres short (Fig. 62b).

Measurements and proportions.— Thirty-seven samples studied, and data for four presented in Tables 25 to 28.

Variation.— A study of this polytypic species is in progress. The following is a summary of more obvious variables. In central Pennsylvania southward, adults are generally golden and only the main mirror is outlined. North of this region to central Minnesota all adults are green. West of this region to central British Columbia adults are either gray-green or bicolored. The bicolored form gradually disappears from British Columbia to northernmost California and Utah. Along the Pacific coast, adults are darker. East of the Cascades, adults become progressively darker southward, and in southern Oregon and adjacent California they are brilliant and almost black. Along the Colorado Plateau, south to northern New Mexico, adults resemble those from British Columbia. From the black form of northern California adults become progressively greener and more densely punctate southward. This last type extends across Nevada to southwestern Wyoming. In central California there is a large form. In the Siskiyou and Trinity Mountain region only, a portion of individuals of this form are bicolored (red-purple elytra).

Table 28. Descriptive statistics for *E. californicus*, based on ten males and ten females from Susanville, California and Quincy, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.65–1.90	1.76	0.114	0.034	4.3
PW	1.75–2.02	1.89	0.136	0.041	4.8
EL	3.85–4.25	4.02	0.200	0.060	3.2
EW	1.52–1.75	1.61	0.090	0.027	3.7
HW	1.87–2.10	1.98	0.100	0.030	3.4
B. Proportions					
PL/PW	0.887–1.000	0.932	0.042	0.012	3.0
PL/EL	0.411–0.463	0.437	0.018	0.006	2.7
PL/EW	1.031–1.134	1.089	0.043	0.014	2.7
PL/HW	0.855–0.938	0.889	0.036	0.010	2.7
PW/EL	0.443–0.488	0.469	0.021	0.006	3.0
PW/EW	1.094–1.231	1.169	0.058	0.018	3.3
PW/HW	0.875–1.012	0.954	0.042	0.012	2.9
EL/EW	2.382–2.576	2.490	0.072	0.022	1.9
EL/HW	1.949–2.125	2.032	0.073	0.022	2.4
EW/HW	0.775–0.875	0.816	0.036	0.010	2.9

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by short epicranial suture (0.2 to 0.3 length of antennomere 1), and by very small anterior seta of abdominal epipleura 1 to 8.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculm serrate. Epicranial suture 0.2 to 0.3 as long as antennomere 1. Seta VEM-p of parietale small. Seta PII-P of nota much longer than that on terga. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleura 1 to 8 subequal and very small.

Second and Third Instar Larvae

Description.— Head brown behind eyes, nota and terga dark brown, and urogomphus brown.

Geographical Distribution and Affinities, and Notes

Distribution.— Transcontinental in North America. It is known almost from the tree line south to extreme southern California, Northern New Mexico, Texas, Louisiana and Florida. Adults were not collected along the Pacific coast Pacific coast north of Washington state (Fig. 172).

Collecting notes.— In most regions, adults are exclusively associated with clay beaches, free of vegetation along creeks, dugouts and ditches. In California adults are found on sandy, silty and clayish beaches. Excluding modified habitats, this species is normally found along small rivers (except for specimens from Pennsylvania southward) where wave and wind action is

Table 29. Descriptive statistics for *E. finitimus*, based on four males and three females from White Mountains, California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.50–1.85	1.65	0.173	0.087	7.0
PW	1.60–2.00	1.81	0.182	0.092	6.7
EL	4.00–4.50	4.27	0.273	0.138	4.3
EW	1.60–1.85	1.72	0.156	0.051	6.0
HW	1.80–2.00	1.89	0.123	0.073	4.3
B. Proportions[1]					
PL/PW		0.910	0.031	0.015	2.3
PL/EL		0.386	0.029	0.014	5.0
PL/EW		0.978	0.041	0.028	2.8
PL/HW		0.884	0.079	0.047	6.0
PW/EL		0.425	0.026	0.013	4.1
PW/EW		1.080	0.024	0.016	1.5
PW/HW		0.979	0.063	0.038	4.3
EL/EW		2.520	0.115	0.077	3.0
EL/HW		2.300	0.116	0.069	3.4
EW/HW		0.902	0.059	0.039	4.4

[1]Values for "Range" not available.

minimal. Beaches are sun-exposed and almost horizontal. Adults run mostly on the moist portions, but avoid the saturated portions.

Taxonomic notes.— The holotype of *E. hesperius* matches adults of the California population, and that of *E. similis* those of Rocky mountain populations.

I have studied about 3000 adults, and dissected more than 100 males. I examined four first instar, eight second instar and six third instar larvae from George Lake, Alberta.

Geographical affinities.— The range of this species overlaps those of all North American species of the subgenus, except that of *E. parviceps*. I have found specimens in a few localities with adults of *E. finitimus, E. americanus* and *E. lecontei,* but, in these situations, adults of these other species were rare. However, I found adults of *E. ruscarius* and of *E. californicus* in equal numbers on clay beaches.

Elaphrus finitimus Casey
Figs. 66a-b, 170

Elaphrus finitimus Casey, 1920:137. Type locality: California; type (seen by me) in United States National Museum of Natural History, Washington, D.C.

Elaphrus ruscarius foveatus Pierce, 1948a:54. Type locality: McKittrick asphalt field, site 4 depth four feet, Los Angeles, California; type (seen by me) in Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

Elaphrus riparius; La Rivers, 1946:138 (*ex parte*) (*nec* Linnaeus, 1758).

Elaphrus americanus; Lindroth, 1961:115 (*ex parte*) (*nec* Dejean, 1831).

Table 30. Descriptive statistics for *E. finitimus*, based on ten males and seven females from Martin Springs, Lassen Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.85	1.68	0.115	0.037	4.6
PW	1.70–2.10	1.88	0.163	0.053	5.8
EL	3.90–4.65	4.32	0.291	0.094	4.5
EW	1.45–1.70	1.60	0.156	0.050	6.5
HW	1.75–1.95	1.84	0.104	0.033	3.8
B. Proportions[1]					
PL/PW		0.897	0.036	0.012	2.7
PL/EL		0.390	0.018	0.006	3.1
PL/EW		1.050	0.083	0.027	5.3
PL/HW		0.911	0.031	0.010	2.3
PW/EL		0.435	0.020	0.006	3.1
PW/EW		1.170	0.109	0.035	6.2
PW/HW		1.010	0.049	0.015	3.2
EL/EW		2.700	0.202	0.065	5.0
EL/HW		2.340	0.105	0.034	3.0
EW/HW		0.868	0.071	0.023	5.4

[1]Values for "Range" not available.

Adults

Diagnostic combination.— Distinguished from adults of all species (excluding *E. americanus*) by character combination in key. From *E. americanus* separated as follows: in males of *E. finitimus,* median lobe long (4.6 to 5.3 mm), and its apex in ventral view thin-edged.

Description.— Two color forms. Green form: microsculptured and smooth surfaces dark copper or black (specimens from Sierra Nevada, White Mountains of California, and northeastern California) dorsally, copper in spots on head and pronotum, and purple near center of pits; punctures green or blue-green (specimens from northeastern California), and purple near center of pits. Ventral coloration as for *E. lecontei.* Copper form (known from Intermontane Region) colored as green form, but punctures generally copper. In both forms: interval 4 of many specimens with purple false pit near main mirror; tibiae red-brown, but metallic at base and apex.

Antennomere 3 with or without few accessory setae. Frons without medial impression, and, in many specimens from northeastern California and adjacent Oregon, with numerous accessory setae. Pronotum with lateral margin slightly convex (Fig. 25), obliterated and not beaded in sinuation, and not explanate before sinuation (Fig. 77d); disc with one or two pairs of submedial impressions, and with accessory setae in some specimens in Intermontane Region. Abdominal sterna with numerous accessory setae between ambulatory setae and lateral punctate area; setae more numerous in males than in most females. Main mirror of elytron rectangular; mirrors in first row generally well outlined, but specimens from Colorado Plateau with two or three rows of sharply delineated mirrors. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly to deeply impressed. Dorso-subapical surface of hind femur with one or two short (40 microns) setae (Fig. 34).

Integument sculpture. Punctures 20 to 25 microns in diameter on head, pronotum and elytra, 30 microns in diameter along outer half of elytral pits and abdominal sterna, and 35 to 40 microns in diameter on thoracic pleura. Punctures 2 to 10 microns apart in elytral pits, portions of pronotum and head, 10 to 20 microns apart on most of elytral intervals 4, 6 and 8 and on proepisternum, and 30 to 40 microns apart antero-laterally on pronotum. First sutural pit of elytron with three to six concentric rows of punctures. Abdominal sternum 3 with 150 to 200 punctures on each side.

Table 31. Descriptive statistics for *E. finitimus*, based on eleven males and nine females from Williams, Arizona.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.57–1.85	1.66	0.099	0.029	4.0
PW	1.67–2.05	1.81	0.134	0.040	4.9
EL	3.90–4.67	4.17	0.258	0.077	4.1
EW	1.45–1.85	1.58	0.135	0.040	5.7
HW	1.75–2.02	1.85	0.099	0.029	3.6
B. Proportions[1]					
PL/PW		0.919	0.043	0.013	3.1
PL/EL		0.399	0.018	0.005	3.0
PL/EW		1.060	0.068	0.020	4.3
PL/HW		0.896	0.027	0.008	2.0
PW/EL		0.434	0.014	0.004	2.1
PW/EW		1.150	0.049	0.015	2.8
PW/HW		0.976	0.039	0.012	2.7
EL/EW		2.650	0.104	0.031	2.6
EL/HW		2.250	0.096	0.029	2.8
EW/HW		0.850	0.048	0.014	3.8

[1]Values for "Range" not available.

Microsculpture outlined over part of or absent from intervals 4, 6 and 8, convex on thoracic pleura, and flat or subconvex (rarely with some pointed microsculpture) on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view thin-edged and twisted, and in lateral view spatulate (Figs. 66a, 66b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view; lobe long: distance from angular bend to apex 4.6 to 5.3 mm. Setae of parameres long (Fig. 69c).

Measurements and proportions.— Twenty samples studied, and data for four presented in Tables 29 to 32.

Variation.— The following is a brief characterization of the seven populations recognized (Goulet and Baum, 1982). The Colorado Plateau form: large; two to three rows of mirrors on elytra; 7% of specimens copper dorsally; accessory setae (seen in few individuals) on pronotum only. The western Great Basin form: dark; accessory setae (in most specimens) on head and pronotum. The White Mountains of California form: almost black; adults of moderate size; head and pronotum without accessory setae. The central California form: punctures dense, all adults green, head and pronotum without accessory setae. The southern California form: similar to that from central California but punctures, especially in elytral pits, much larger. In southern Sierra Nevada a dark and deeply pitted form with large punctures in pits is found. The sample from northwestern Arizona resembles those of central California, but differs from them in having 30% of specimens copper.

Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by character combination in key.

Table 32. Descriptive statistics for *E. finitimus*, based on seven males and twelve females from Sonoma Co., California and Marin Co., California.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.60–1.75	1.67	0.069	0.021	2.7
PW	1.70–1.90	1.80	0.100	0.030	3.7
EL	3.75–4.35	4.11	0.237	0.072	3.8
EW	1.50–1.90	1.60	0.096	0.029	4.0
HW	1.80–1.90	1.85	0.057	0.017	2.1
B. Proportions[1]					
PL/PW		0.929	0.042	0.013	3.1
PL/EL		0.405	0.018	0.006	3.0
PL/EW		1.040	0.057	0.017	3.7
PL/HW		0.900	0.030	0.009	2.2
PW/EL		0.438	0.024	0.007	3.6
PW/EW		1.120	0.053	0.016	3.2
PW/HW		0.970	0.044	0.013	3.0
EL/EW		2.570	0.138	0.042	3.6
EL/HW		2.220	0.090	0.028	2.7
EW/HW		0.864	0.041	0.013	3.2

[1]Values for "Range" not available.

Description.— Very similar to same instar of *E. americanus* except microsculpture on tergal bands more restricted: pointed microsculpture on about 50% of posterior band laterally, and absent from anterior band.

Geographical Distribution and Affinities, and Notes

Distribution.— A western North American species associated with forested regions, from southern Oregon to western Montana in the north, to southernmost California, northern Arizona and southern Colorado in the south (Fig. 170).

Collecting notes.— I collected large series of this species around Petaluma, California on wet clay beaches. Beaches were sun-exposed, protected from winds and strong wave action, and free of vegetation. I have no data from other areas of its range, though G.E. Ball (pers. comm.) collected one adult from southern Idaho in a similar habitat.

Taxonomic notes.— The fossil specimen of *E. ruscarius foveatus* is represented by one complete elytron. The elytron best matches that of *E. americanus* or *E. finitimus*. Microsculpture, puncture density on elytral intervals 4, 6 and 8 and shape of pit behind main mirror suggest the above association. I am not able to ascertain which of the two species this elytron represents but it matches perfectly extant western Californian specimens of *E. finitimus*.

I have studied about 1000 adults and dissected more than 100 males. I examined one third instar larva.

Geographical affinities.— The range of *E. finitimus* overlaps those of *E. marginicollis, E. viridis, E. mimus, E. lecontei* and *E. californicus*. In the same habitat few specimens of *E.*

californicus may be found with those of *E. finitimus*.

Elaphrus americanus Dejean

Adults

Diagnostic combination.— Distinguished from adults of all species (except those of *E. finitimus*) by character combination in key. Distinguished from adults of *E. finitimus* as follows. In males of *E. americanus,* median lobe short (3.5 to 4.7 mm), and its apex in ventral view thick-edged (Figs. 67a, 68a, 69a).

Variation.— Goulet and Baum (1981) distinguished two subspecies. One is restricted to boreal regions, from the arctic treeline south to central British Columbia, and east to Newfoundland. The other extends along the Pacific coast from British Columbia to southern Oregon, eastward across southern British Columbia to southwestern Alberta, south to northeastern Oregon, central Idaho and central Colorado. These subspecies are best defined by the ratio (PL/HW). The mean for samples (17) of the boreal subspecies is significantly smaller (mean range: 0.851 to 0.882 - average for all samples 0.864) than those (22) of the western subspecies (mean range; 0.884 to 0.916-average for all samples 0.896). The ranges of variation in means between samples show no geographical pattern for each subspecies. Based on above measurements, the two subspecies are characterized in a discriminant function allowing correct identification of 78% of individuals (Goulet and Baum, 1981). Moreover, the above function in combination with other characters mentioned below should allow correct identification of each specimen. Because the differences observed are maintained even when both subspecies are adjacent in their ranges, and because there is no clinal variation in character states studied, subspecific rank is given to these two populations. However, the results of various analyses clearly point out that *E. americanus* is probably a superspecies (Goulet and Baum, 1981) including two allopatric species, but more collecting is needed to determine rank of these taxa.

Elaphrus americanus americanus Dejean
Figs. 32, 34, 69a-c, 100a-b, 117, 128, 135, 170

Elaphrus americanus Dejean, 1831:558. Type locality: Great Bear Lake, Northwest Territories, subsequently designated by Lindroth (1961); type (seen by Lindroth) in Museum National d'Histoire Naturelle, Paris. Lindroth, 1961:115 *(ex parte)*.

Elaphrus intermedius Kirby, 1837:62. Type locality: Great Bear Lake, Northwest Territories; type (seen by Lindroth) in British Museum of Natural History, London. Walker, 1866:309 *(ex parte)*. Crotch, 1876:246; Schaupp, 1878:6. Lindroth, 1961:115.

Elaphrus punctatissimus LeConte, 1850:210. Type locality: Sault Ste. Marie, Michigan; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:401. Schaupp, 1878:6. Lindroth, 1961:115.

Elaphrus sinuatus LeConte, 1850:210. Type locality: Pic, Ontario (north shore of Lake Superior); type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. LeConte, 1853:402. Lindroth, 1961:115.

Elaphrus gratiosus Mannerheim, 1853:118. Type locality: Kaktnu River, Kenai peninsula, Alaska; type (seen by Lindroth) in Zoological Museum, University, Helsinki. Schaupp, 1878:6. Lindroth, 1961: 115.

Elaphrus riparius; Crotch, 1873:4 *(ex parte)*. 1876:246 *(ex parte)*. Schaupp, 1878:6 *(ex parte)*. Taylor, 1886:35 *(ex parte)*. Harrington, 1889:139 *(ex parte)*. Venables, 1913:26 *(ex parte)*. Hippisley, 1922:63 *(ex parte)*. Van Dyke, 1924:3. Guppy, 1947:51. Clark, 1948:25 *(ex parte)*. Hatch, 1953:63 *(ex parte)*. *nec* Linnaeus, 1758.

Elaphrus bituberosus Casey, 1924:17. Type locality: Terrace, British Columbia; lectotype (seen by me) designated by Lindroth (1976:113) in United States National Museum of Natural History, Washington, D.C. Lindroth, 1961:115.

Table 33. Descriptive statistics for *E. americanus americanus*, based on 14 males and six females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.40–1.67	1.54	0.114	0.034	4.9
PW	1.52–1.82	1.64	0.147	0.044	6.0
EL	3.60–4.50	4.03	0.345	0.103	5.7
EW	1.35–1.70	1.48	0.152	0.045	6.8
HW	1.70–1.92	1.79	0.107	0.033	4.0
B. Proportions[1]					
PL/PW		0.936	0.043	0.013	3.1
PL/EL		0.382	0.019	0.006	3.4
PL/EW		1.040	0.068	0.020	4.3
PL/HW		0.862	0.031	0.009	2.4
PW/EL		0.408	0.020	0.006	3.3
PW/EW		1.110	0.054	0.016	3.2
PW/HW		0.922	0.037	0.011	2.7
EL/EW		2.720	0.110	0.033	2.7
EL/HW		2.250	0.106	0.032	3.1
EW/HW		0.831	0.053	0.016	4.3

[1]Values for "Range" not available.

Adults

Diagnostic combination.— Recognized from adults of *E. americanus sylvanus* as follows: Accessory setae abundant on antennomere 3 (more than one seta per sample on average) and on metepisternum (few to numerous setae); pronotum relatively short (PL) and in combination with HW the ratio PL/HW smaller than 0.883 on average per sample (for discriminant function based on the same variables see Goulet and Baum, 1981); punctures of elytral intervals 4 dense (less than 40 microns apart on average per sample); foretibial sulcus (groove parallel to fringe) expressed in most specimens, but well developed in few; mirrors of elytron confluent in few specimens; apex of median lobes of males, in lateral view narrow, and in ventral view, straight (Figs. 69a, 69b).

Description.— Two color forms (in some samples intermediate known). For details see *E. lecontei* (p. 295).

Antennomere 3 of most specimens with accessory setae (Fig. 12). Frons without medial impression, and without accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc with one or two pairs of submedial impressions and with accessory setae in many specimens. Abdominal sterna with numerous accessory setae between ambulatory setae and lateral punctate area; setae more numerous in males than in most females. Main mirror of elytron rectangular; one to three rows of mirrors or only main mirror sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

Integument sculpture. Punctures 25 microns in diameter on dorsal body surface, and 30 to 35 microns in diameter ventrally. Punctures 2 to 10 microns apart in elytral pits, 10 to 60 microns apart on intervals 4, 6 and 8, about 20 microns apart submedially and 40 microns apart antero-laterally on pronotum, and 10 to 20 microns apart on proepisternum. First sutural pit of elytron with three to six concentric rows of punctures. Abdominal sternum 3 with 100 to 200 punctures on each side.

Microsculpture flat or absent from elytral intervals, pronotum and head; convex on thoracic pleura, and flat (with a few points in basal area) on abdominal sterna between ambulatory setae and punctate area.

Male genitalia. Apex of median lobe in ventral view thick-edged and straight, and in lateral view narrowly spatulate (Figs. 69a, 69b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a); lobe shorter between angular bend and apex (3.5 to 4.7 mm). Setae of parameres long (Fig. 69c).

Measurements and proportions.— Eighteen samples studied, and data for one presented in Table 33.

Variation.— Members of this subspecies appear homogeneous except for those in northwestern North America. Adults from this region are small in most measurements (see PL and PW in Goulet and Baum (1981) in Table 5), show a low ratio PL/PW (smaller than 0.405), have generally no foretibial sulcus, have dense punctures on elytral interval 4 (15 to 20 microns apart on average per sample studied), have many concentric rows of punctures (greater than 4.3 on average per sample studied) in the first pit near the suture, and have the accessory setae of abdominal sterna closer to the lateral punctate area. However, in most of these characters, samples from northern British Columbia, central and northern Alberta, and western Northwest Territories are intermediate between Beringian samples and those farther south. Therefore, I do not consider these populations as subspecifically distinct.

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by character combination in key.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Seta VEMP-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AIM on terga abruptly short, at least on tergum 8. Antero-dorsal seta on epipleura very small on segments 8, or 7 and 8, and larger on anterior segments.

Second and Third Instar Larvae

Description.— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

Geographical Distribution and Affinities, and Notes

Distribution.— Transamerican in forested areas of boreal regions, but not reaching the Pacific coast except in southwestern Alaska (Fig. 1; see Goulet and Baum, 1981).

Collecting notes.— Adults are regularly found on wet beaches along slow meandering creeks. The beach is almost horizontal and consists of organic, coarse and quite firm soil. The surface is sun-exposed and sheltered from winds. This habitat is regularly found around beaver ponds.

Taxonomic notes.— Holotypes studied of conspecific forms mentioned above match typical specimens of this subspecies. I studied more than 2000 adults, and dissected more than 300 males. I examined five first instar, eight second instar, and five third instar larvae from George Lake, Alberta.

Geographical affinities.— The range of this subspecies overlaps widely those of *E. californicus* and *E. tuberculatus,* and marginally those of *E. ruscarius* and *E. finitimus.* I have often seen adults of *E. californicus* with those of this subspecies, but in all instances those of one species was overwhelmingly dominant. Once, I found adults of this subspecies, *E. californicus* and *E. lecontei* on the same beach where the three habitats were found within 10 m, but adults of each species remained mainly in their respective habitat.

Table 34. Descriptive statistics for *E. americanus slyvanus*, based on ten males and ten females from Pullman, Washington.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.55–1.85	1.69	0.134	0.040	5.3
PW	1.65–2.05	1.82	0.164	0.049	6.0
EL	3.80–4.65	4.27	0.344	0.102	5.4
EW	1.45–1.82	1.60	0.169	0.050	7.0
HW	1.75–2.00	1.88	0.115	0.034	4.1
B. Proportions[1]					
PL/PW		0.929	0.036	0.011	2.6
PL/EL		0.396	0.019	0.006	3.2
PL/EW		1.050	0.060	0.018	5.7
PL/HW		0.897	0.029	0.009	2.1
PW/EL		0.427	0.020	0.006	3.1
PW/EW		1.140	0.057	0.017	3.3
PW/HW		0.966	0.046	0.014	3.2
EL/EW		2.660	0.102	0.030	2.6
EL/HW		2.270	0.098	0.029	2.9
EW/HW		0.852	0.052	0.015	4.1

[1]Values for "Range" not available.

Elaphrus americanus sylvanus Goulet
Figs. 67a-b, 68a-b, 170

Elaphrus americanus sylvanus Goulet, in Goulet and Baum, 1981:2271. Type locality: Oregon, Coos Co., 16 mi. N of Powers; holotype (No. 18011) in the Canadian National Collection, Ottawa.

Adults

Diagnostic combination.— Distinguished from adults of *E. americanus americanus* as follows: Accessory setae few on antennomere 3 (less than two setae on average per sample) and on metepisternum (most specimens without setae); pronotum relatively long (PL) and in combination with HW the ratio PL/HW greater than 0.884 on average per sample (for discriminant function based on the same variables see Goulet and Baum, 1981). For populations adjoining the range of *E. americanus americanus* (southern British Columbia and Alberta), punctures of elytral interval 4 scattered (more than 40 microns apart on average per sample); foretibial sulcus (groove parallel to fringe) well developed in most specimens; mirrors of elytron generally more confluent. Apex of median lobe of males, in lateral view, narrow (Fig. 68b) (Pacific coast, Cascades, and western Oregon populations) or wide (Fig. 67b) (elsewhere), and in ventral view, straight (Fig. 68a) (Pacific coast, Cascades, and western Oregon populations – with occasional specimens in other populations) or slightly twisted (Fig. 67a) (other populations).

Description.— Similar to specimens of *E. americanus americanus* except the following. Color: as for *E. americanus americanus* except for dark specimens from Mount Hood, Oregon and northeastern Oregon with microsculptured and smooth surfaces black and punctures blue-green.

Antennomore 3 of most specimens without accessory setae. Elytral pits slightly to deeply impressed. Punctures 10 to 100 microns apart on intervals 4, 6 and 8. Apex of median lobe in ventral view slightly twisted or straight, and in lateral view widely to narrowly spatulate (Figs. 67a, 67b, 68a, 68b).

Measurements and proportions.— Twenty-two samples studied, and data for one presented in Table 34.

Variation.— Seven populations are recognized: Pacific coast, Cascades, Mount Hood, Willamette Valley, northern Great Basin, northeastern Oregon, and central Rocky Mountains. There is no evidence of clinal variation among them, and their status as species or subspecies is therefore uncertain. These populations are characterized in Goulet and Baum (1981).

All Instar Larvae

Diagnostic combination.— The few specimens studied match those of *E. americanus americanus.*

Geographical Distribution and Affinities, and Notes

Distribution.— In forested regions, from the Pacific coast along British Columbia to southern Oregon, eastward across southern British Columbia to southwestern Alberta, south to northeastern Oregon, central Idaho, and central Colorado. (Fig. 1; see Goulet and Baum, 1981).

Collecting notes.— In coastal Oregon, adults were found on clay beaches on the saturated portion. The habitat is similar to that of *E. californicus* except that adults run mostly on the saturated portion of the beach. However, in the Cascades, adults of the subalpine form are found in many localities running around snow surfaces on bare organic soil or on matted vegetation.

Taxonomic notes.— I studied about 1000 adults, and dissected more than 100 males. I examined one first instar and one third instar larva from Mount Rainier, Washington, and one third instar larva from the type locality near Powers, Oregon.

Geographical affinities.— The range of this subspecies overlaps widely with that of *E. californicus,* and marginally with those of *E. finitimus* and *E. marginicollis.*

Elaphrus comatus new species
Fig. 63a-b

Elaphrus riparius Nakane, 1963:19. Ohkura, 1973:5. *nec* Linnaeus, 1758.

Elaphrus comatus new species. Type material: holotype male and allotype female labelled "No CHINA:, P.M. Hammond., B.M. 1967-215. Heilung kiang, Harbin, 12.6.66"; type deposited in British Museum (Natural History), London.

Adults

Diagnostic combination.— Distinguished from adults of other Asiatic species by many long setae on dorso-apical surface of hind femur, and in lateral view by subtruncated apex of median lobe of males (Fig. 63b).

Description.— Only green specimens seen. For details about coloration see under *E. lecontei* (p. 295).

Antennomere 3 with few accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc without or with one or two pairs of submedial impressions(Fig. 25). Abdominal sterna of both sexes with abundant accessory setae extended to edge of sterna 5 and 6. Main mirror of elytron rectangular; main mirror sharply outlined,

Table 35. Descriptive statistics for *E. comatus*, based on three males and six females from Japan (Muki) and China (Harbin).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.35–1.50	1.46	0.081	0.036	3.7
PW	1.55–1.70	1.61	0.081	0.036	3.4
EL	3.75–4.10	3.99	0.179	0.080	3.0
EW	1.42–1.62	1.54	0.106	0.047	4.6
HW	1.67–1.77	1.74	0.053	0.024	2.0
B. Proportions					
PL/PW	0.868–0.952	0.907	0.043	0.020	3.2
PL/EL	0.359–0.375	0.367	0.009	0.004	1.6
PL/EW	0.923–0.999	0.948	0.034	0.016	2.4
PL/HW	0.800–0.870	0.840	0.034	0.016	2.7
PW/EL	0.394–0.420	0.405	0.012	0.006	1.9
PW/EW	1.000–1.098	1.046	0.046	0.020	3.0
PW/HW	0.900–0.971	0.927	0.031	0.014	2.3
EL/EW	2.500–2.690	2.585	0.084	0.038	2.2
EL/HW	2.229–2.319	2.290	0.051	0.022	1.5
EW/HW	0.851–0.915	0.886	0.039	0.018	2.9

others suggested or absent. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and impressed in basal half. Dorso-subapical surface of hind femur with many long (100 to 150 microns) setae (Fig. 35).

Integument sculpture. Punctures 20 to 25 microns in diameter on elytra, pronotum and head, 30 microns in diameter in elytral pits, and 30 to 35 microns in diameter on thoracic pleura. Punctures 10 to 20 microns apart on elytron, 5 to 10 microns apart in pits, 10 to 20 microns apart submedially and 30 to 50 microns apart laterally on pronotum, and 20 to 30 microns apart on proepisternum. First sutural pit of elytron with three to four concentric rows of punctures. Abdominal sternum 3 with 50 to 70 punctures on each side.

Microsculpture convex dorsally and absent in spots, convex on thoracic pleura, and flat on abdominal sterna (surface brilliant).

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted, and in lateral view truncate (Figs. 63a, 63b); base of lobe along ventral angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61a). Setae of parameres long (Fig. 69c).

Measurements and proportions.— One sample studied, see Table 35.

Variation.— Samples from northeastern China and Japan appear similar. Unfortunately these samples are too small for analysis.

Derivation of specific epithet.— From Latin *comatus* meaning long-haired, referring to long setae on dorso-subapical surface of hind femur.

Distribution.— Known from northeastern China and Japan.

China. - HEILUNG KIANG: Harbin (7:BMNH).

Japan. - Muki (2:CASC)

Geographical affinities.— To my knowledge, the range of this species does not overlap with those of other species unless the range of *E. riparius* extends to the Pacific coast.

Table 36. Descriptive statistics for *E. riparius*, based on ten males and ten females from Silvakra, Skane, Sweden.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.30–1.67	1.51	0.126	0.038	5.6
PW	1.40–1.87	1.66	0.178	0.053	7.1
EL	3.30–4.25	3.92	0.332	0.099	5.6
EW	1.25–1.67	1.51	0.168	0.050	7.4
HW	1.60–1.97	1.77	0.144	0.043	5.4
B. Proportions					
PL/PW	0.840–0.953	0.909	0.039	0.012	2.9
PL/EL	0.371–0.400	0.384	0.012	0.004	2.1
PL/EW	0.940–1.067	1.002	0.054	0.016	3.6
PL/HW	0.812–0.877	0.849	0.025	0.008	2.0
PW/EL	0.401–0.446	0.423	0.018	0.003	2.8
PW/EW	1.050–1.167	1.103	0.045	0.014	2.7
PW/HW	0.875–1.000	0.935	0.040	0.012	2.9
EL/EW	2.476–2.755	2.606	0.120	0.036	3.1
EL/HW	2.062–2.313	2.209	0.091	0.028	2.8
EW/HW	0.781–0.893	0.848	0.042	0.012	3.3

Elaphrus riparius (Linnaeus).
Figs. 11, 25, 61a-b, 141, 143, 153

Cicindela riparia Linnaeus, 1758:407. Type locality: Uppsala, Sweden -- designated subsequently by Lindroth (1961); type (seen by Lindroth) in Linnean Collection, London. Poda, 1761:42. Müller, 1764:18, 178. De Geer, 1774:117. Müller, 1776:80, 864. Schrank, 1781:192. Thomson, 1859:3, 194.

Elaphrus riparius; Fabricius, 1775:227. Panzer, 1793:20. Illiger, 1798:225. Geoffroy, 1799:156 *(ex parte)*. Fabricius, 1801:245. Latreille, 1804:217. 1806:227. 1810:425. Gyllenhal, 1810:6. Dejean, 1826:274. Curtis, 1827:179. Gyllenhal, 1827:397. Erichson, 1837:4. Heer, 1838:39. Schiødte, 1841:356. Küster, 1846:7. Letzner, 1849:51. Fairmaire and Laboulbène, 1854:6. Schaum, 1856:72. Stierlin, 1869:11. Solsky, 1872:233. Redtenbacher, 1874:6. Seidlitz, 1875:2. Mäklin, 1877:17. Dalla-Torre, 1877:23. Sahlberg, 1880:10 *(ex parte)*. Bedel, 1881:23. Fauvel, 1882:82, 84. Marseul, 1882:4. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:316. Everts, 1898:48. Semenov, 1904b:125. 1904a:20; Jacobson, 1906:267. Reitter, 1908:96, 97. 1909:105. Kuhnt, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Bänninger, 1919:148. Porta, 1923:78. Semenov, 1926:40. Portevin, 1929:41. Jacobson, 1931:82. Joy, 1932:328. Lindroth, 1939:62 - 67. Jeannel, 1941:217. Smetana, 1951:232. Lindroth, 1957:339. 1961: 115 *(ex parte)*. 1974:33.

Elaphrus paludosus Olivier, 1790:5. Type locality: Paris, France; type not seen. Latreille, 1804:217. 1806:227. Dejean, 1826:274. Schaum, 1856:72. Marseul, 1882:4. Ganglbauer, 1892:123, 124. Semenov, 1895:315. 1904a:20. Jacobson, 1906:267. Jeannel, 1941:217.

Elaphrus dilaticollis R.F. Sahlberg, 1844:22. Type locality: Okhotsk Sea, USSR; type not seen. Marseul, 1880:31. 1882:4. Semenov, 1895:316. Jacobson, 1906:267.

Elaphrus violaceomaculatus Motschulsky, 1845:337. Type locality: Kamchatka, USSR; type not seen. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

Elaphrus baschkiricus Motschulsky, 1846:72. Type locality: Orenburg, Baschkir Aut Rep., USSR; type not seen. Marseul, 1882;4. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

Elaphrus riparius var. *nigrescens* Letzner, 1849:52. Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen. Jacobson, 1906:267.

Elaphrus riparius var. *viridis* Letzner, 1849:52. Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen.

Jacobson, 1906:267. Csiki 1927:92. Lindroth, 1961:110.

Elaphrus riparius var. *smaragdinus* Letzner, 1849:52 (name attributed to Müller, but to my knowledge never published). Type locality: Wroclaw, Poland (Silesia, Breslau); type not seen. NEW SYNONYM.

Elaphrus latiusculus Motschulsky, 1850a:5. Type locality: Dauria (southeast of Lake Baikal), USSR; type not seen. Marseul, 1880:32. 1882:4. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267.

Elaphrus riparius var. *violaceomaculatus; Marseul, 1882:4.*

Elaphrus californicus; Ganglbauer, 1892:123. Semenov, 1895:315. 1904a: 20. Jacobson, 1906:267. Hatch, 1953:63. *nec* Mannerheim, 1843.

Elaphrus punctatissimus; Ganglbauer, 1892:123. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. Hatch, 1953:63. *nec* LeConte, 1850.

Elaphrus intermedius; Ganglbauer, 1892:123, 124. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* Kirby, 1837.

Elaphrus similis; Ganglbauer, 1892:123, 124. Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* LeConte, 1848.

Elaphrus sinuatus; Ganglbauer, 1892:123, 124; Semenov, 1895:316. 1904a: 20. Jacobson, 1906:267. *nec* LeConte 1850.

Elaphrus gratiosus; Semenov, 1895:316. 1904a:20. Jacobson, 1906:267. *nec* Mannerheim, 1853.

Elaphrus trossulus Semenov, 1904a:21. Type area: Western Mongolia: type not seen. Jacobson, 1906:267. Bänninger, 1919:148 (suggested synonym).

Elaphrus riparius ab. *atratulus* Wagner, 1917:259. Type locality: Brieslang, Germany; type not seen. Bänninger, 1919:148.

Elaphrus riparius ab. *cupritarsis* Bänninger, 1919:148. Type area: Turkestan; type does not exist. Name accidentally validated by Bänninger's discussion of Reitter's sample with the unpublished name attached to specimens.

Elaphrus riparius ab. *rubescens* Antoine, 1920:9. Type locality: between Berk-plage and Merlimont (Pas-de-Calais), France; type not seen.

Elaphrus bituberosus; Hatch, 1953:63 (*nec* Casey, 1924).

Adults

Diagnostic combination.— Among species with expanded accessory setae on abdominal sterna, specimens of this species are separated from those of *E. parviceps* and *E. tibetanus* by more abundant punctures on abdominal sterna, and from those of *E. comatus* by shorter and fewer dorso-subapical setae on hind femur; they are separated from adults of *E. tuberculatus* with difficulty using the character combination in the key.

Description.— Two color forms: green and copper. For details see under *E. lecontei* (p. 295).

Antennomere 3 without accessory setae apically (Fig. 11). Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d), disc without or with one pair of weakly outlined submedial impressions, and with accessory setae on some specimens in central Asia. Abdominal sterna of both sexes with abundant accessory setae extended into lateral punctate area of segments 5 and 6. Main mirror of elytron rectangular; main mirror only, or mirror of first row, or exceptionally mirrors in two or three rows, sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

Integument sculpture. Punctures 20 to 25 microns in diameter on elytral intervals, pronotum and head, 30 microns in diameter on outer half of each elytral pit and abdominal sterna, and 30 to 40 microns in diameter on thoracic pleura. Punctures 5 to 10 microns apart in elytral pits, 10 to 20 microns apart on elytral intervals 4, 6 and 8, 15 to 20 microns apart submedially and 30 to 40 microns apart antero-laterally on pronotum, and 30 microns apart on proepisternum. First sutural pit of elytron with four to five concentric rows of punctures. Abdominal sternum 3 with 50 to 80 punctures.

Microsculpture subconvex dorsally, convex in elytral pits, and on thoracic pleura, and forming sharp prominent scales between ambulatory setae and edge of abdominal sterna 5 and 6 in most specimens (best seen in diffused light, see Figs. 143 and 153).

Male genitalia. Apex of median lobe in ventral view edged and twisted, and in lateral view spatulate (Figs. 61a, 61b); base of lobe along angular bend narrowly sclerotized, and ventral membrane visible in lateral view (Fig. 61b). Setae of parameres long (Fig. 69c).

Measurements and proportions.— Three samples studied, and data for one presented in Table 36.

Variation.— As more material was needed, I did not attempt a detailed analysis of variation among populations of this species. However, the differences observed suggest a species complex. Specimens from southern Europe are generally golden green and dull, and those from western China and western USSR have accessory setae on the pronotum. In addition, as discovered by Smetana (1951), there is the possibility of isolated high altitude populations that may be in the process of differentiation (on this topic see Goulet and Baum, 1981). A study of this complex is

best suited for a student with access to large Palaearctic collections.

All Instar Larvae

Diagnostic combination.— Recognized from larvae of other species by character combination in key.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculum smooth. Epicranial suture 0.3 to 0.4 as long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AII and AIM on nota small. Seta AIM on terga 1 to 8 subequal. Antero-dorsal seta of abdominal epipleuron very small on segment 8, or on 7 and 8, and markedly larger on other segments.

Second and Third Instar Larvae

Description.— Head brown behind eyes, and nota, terga and urogomphus dark brown.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of this species extends into cold temperate and boreal regions of the Palaearctic Region, from the Atlantic coast as far east as western China, Mongolia and Lake Baikal. Records of this species along the Pacific coast probably refer to *E. comatus*. I have seen specimens from almost every European country reported by Lindroth (1945) and from central Asia.

Collecting notes.— Adults were collected on the moist and wet portions of sandy and clayish beaches along rivers, ditches, etc. Beaches were sun-exposed, and the vegetation scattered or absent. Adults are rarely found on organic, peaty, gravelly or rocky shores (Lindroth 1945).

Taxonomic notes.— The separation of adults of this species from those of *E. tuberculatus* is extremely difficult as pointed out by Lindroth (1939). I discovered independently the differences he observed, and confirmed his general conclusions. These differences are maintained across the range of both species. Moreover, larvae of *E. tuberculatus* (North American sample) and those of *E. riparius* (from Austria) are probably the most distinctive larvae of the subgenus. Therefore, I feel there is sufficient evidence to recognize *E. tuberculatus* as specifically distinct from *E. riparius*.

As no types were seen, the above synonymy is tentative. Based on descriptions of type series and their type localities, the following names are probably synonymous with *E. riparius: E. paludosus, E. baschkiricus* and *E. latiusculus*. Similarly, the following names are probably synonymous with *E. riparius,* and may represent only color variants: *E. riparius* var. *nigrescens, E. riparius,* var. *viridis, E. riparius* var. *smaragdinus, E. riparius* ab. *atratulus, E. riparius* ab. *cupritarsis* and *E. riparius* ab. *rubescens*. *E. riparius* ab. *atratulus* may be a local color variant or a postmortem color change. Semenov (1895) suggested that *E. violaceomaculatus* and *E. dilaticollis* are synonymous with *E. riparius*. However, the type localities of these insects suggest perhaps a relation to the North American *E. tuberculatus* (see comments under this species). *E. trossulus,* based on Bänninger's specimens, represents a geographical variant of *E. riparius*. Bänninger's specimens fit Semenov's original (1904a) description perfectly.

I studied about 500 specimens, and dissected ten males. I examined three first instar, two second instar and three third instar larvae from Austria.

Geographical affinities.— The range of *E. riparius* overlaps those of *E. hypocrita* and *E. tuberculatus*.

Table 37. Descriptive statistics for *E. tuberculatus*, based on ten males and ten females from Sorcele, Sweden.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.67	1.53	0.100	0.030	4.3
PW	1.52–1.85	1.70	0.133	0.040	5.2
EL	3.75–4.50	4.17	0.283	0.084	4.5
EW	1.40–1.70	1.54	0.112	0.030	4.8
HW	1.67–1.97	1.82	0.112	0.034	4.1
B. Proportions					
PL/PW	0.811–0.954	0.904	0.051	0.016	3.8
PL/EL	0.333–0.390	0.368	0.022	0.006	4.0
PL/EW	0.882–1.050	0.992	0.054	0.016	3.6
PL/HW	0.759–0.875	0.841	0.042	0.012	3.3
PW/EL	0.387–0.432	0.407	0.017	0.006	2.7
PW/EW	1.048–1.167	1.098	0.040	0.012	2.4
PW/HW	0.871–0.986	0.931	0.040	0.012	2.9
EL/EW	2.623–2.807	2.698	0.081	0.024	2.0
EL/HW	2.143–2.417	2.289	0.111	0.032	3.2
EW/HW	0.800–0.880	0.849	0.035	0.010	2.7

Elaphrus tuberculatus Mäklin.
Fig. 171

Elaphrus tuberculatus Mäklin, 1877:16. Type locality: Brochowsky Island (70° 39′ N) in Yenisey River, USSR; type not seen. Sahlberg, 1880:11. Jacobson, 1906:267. Semenov, 1909:433. Bänninger, 1919:148. Semenov, 1926:40. Bänninger, 1931:184.

Elaphrus latipennis J. Sahlberg, 1880:10. Type locality: Dudinka, USSR; type not seen. Semenov, 1904a:20. Jacobson, 1906:267. Semenov, 1909:433.

Elaphrus riparius; Sahlberg, 1880:10 *(ex parte)*. Lindroth, 1961:116 *(ex parte)*. *nec* Linnaeus, 1758.

Elaphrus latipennis var. *orientalis* Semenov, 1904a:20. Type locality: Bulun (lower Lena River), USSR; type not seen. Jacobson, 1906:267. Semenov, 1909:433.

Elaphrus latipennis ab. *costulifer* Semenov, 1904b:125. Type area: Arctic region of Kanin and Kolgujev, USSR; type not seen. Semenov, 1904a:20. Jacobson, 1906:267.

Elaphrus latipennis ab. *normalis* Poppius, 1908:4. Type locality: not known to me; type not seen. Semenov, 1909:433.

Elaphrus tuberculatus ab. *costulifer;* Semenov, 1909:433.

Elaphrus tuberculatus var. *orientalis;* Semenov, 1909:433.

Elaphrus tumidiceps Munster, 1924:288. Type locality: Lakselv in Porsanger, Norway; type (seen by Lindroth) in Oslo, Norway. Bänninger, 1931:184; Lindroth, 1939:62 - 67.

Elaphrus riparius tuberculatus; Lindroth, 1939:62 - 67.

Adults

Diagnostic combination.— Distinguished from adults of *E. comatus, E. parviceps* and *E. tibetanus* by character combination described under *E. riparius*. This species is separated from *E. riparius* using character combination in key.

Description.— Two color forms. For details see *E. lecontei* (p. 295), except the following. Tibiae metallic on dorsal surface of most specimens.

Table 38. Descriptive statistics for *E. tuberculatus*, based on ten males and ten females from Inuvik, N.W.T.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.32–1.55	1.44	0.115	0.034	5.3
PW	1.45–1.72	1.60	0.121	0.036	5.1
EL	3.50–4.50	4.01	0.371	0.111	6.2
EW	1.37–1.65	1.50	0.119	0.036	5.3
HW	1.60–1.82	1.73	0.081	0.024	3.1
B. Proportions					
PL/PW	0.855–0.938	0.899	0.037	0.012	2.8
PL/EL	0.329–0.401	0.359	0.025	0.008	4.7
PL/EW	0.900–1.036	0.958	0.057	0.016	4.0
PL/HW	0.768–0.870	0.830	0.046	0.014	3.7
PW/EL	0.382–0.432	0.399	0.019	0.006	3.2
PW/EW	1.032–1.117	1.066	0.040	0.012	2.5
PW/HW	0.896–0.970	0.924	0.039	0.012	2.8
EL/EW	2.500–2.828	2.672	0.115	0.034	2.9
EL/HW	2.088–2.500	2.316	0.142	0.042	4.1
EW/HW	0.809–0.939	0.867	0.051	0.016	3.9

Antennomere 3 without or with accessory setae (Fig. 11 and 12). Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25 and 77d); disc without or with one pair of submedial impressions and with accessory setae in few specimens. Abdominal sterna in both sexes with abundant accessory setae extended to edge of sterna 5 and 6. Main mirror of elytron rectangular; mirrors of first two or three rows sharply outlined. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

Integument sculpture. Puncture diameter as for *E. riparius,* except 20 to 30 microns across dorsally. Punctures generally less dense than in *E. riparius:* 10 to 25 microns apart in first sutural pit of elytron, and 15 to 30 microns apart on intervals. First sutural pit of elytron with four or five concentric rows of punctures. Abdominal sternum 3 with 40 to 80 punctures on each side.

Microsculpture generally convex on dorsal and pleural surfaces (dull reflection), convex on abdominal sterna, and with or without raised sharp scales basally (rarely expanded as in *E. riparius*).

Male genitalia. In every detail as that of *E. riparius* (Figs. 61a, 61b, 69c).

Measurements and proportions.— Three samples studied, and data for two presented in Tables 37 and 38.

Variation.— Between northern Scandinavian and eastern Siberian samples, I observed few differences. In eastern Siberia, 10% of adults have accessory setae on the pronotum, most have some accessory setae on the antennomere 3, and punctures are large on the pronotum (about 30 microns in diameter). In Scandinavia, adults have no accessory setae on the pronotum or on antennomere 3, and punctures are small on the pronotum (about 25 microns in diameter). Many specimens of both regions are copper in color. In North America, adults differ in many characteristics from Palaearctic samples: no copper individuals, punctures dense (15 to 20 microns apart) on the pronotum submedially, and only mirrors of the first row, or the main mirror, sharply outlined. Adults of this species in the Nearctic region are strictly riparian while

those in the Palaearctic region are not, as suggested by notes on habitat (Lindroth, 1939, 1945). Finally the Scandinavian sample has a significantly larger mean for ratio PL/EW than those of other two samples. The limited data suggest that *E. tuberculatus* is a complex of taxonomically distinct forms.

All Instar Larvae

Diagnostic combination.— Recognized from larvae of other species by character combination in key.

First Instar Larvae

Description.— Apical inner margin of mandible and posterior margin of retinaculum serrate. Epicranial suture 0.4 to 0.5 long as antennomere 1. Seta VEM-P of parietale small. Seta PII-P on nota much longer than that on terga. Seta AIM on terga subequal. Antero-dorsal seta of abdomial epipleuron very small on segments 8, or 7 and 8, and markedly longer on other segments.

Second and Third Instar Larvae

Description.— Head pale at base and behind eyes, nota and terga dark brown, and urogomphus pale.

Geographical Distribution and Affinities, and Notes

Distribution.— This is a Holarctic species found from northern Scandinavia to eastern Siberia in southern arctic regions of the Palaearctic Region, and from Alaska to the MacKenzie River in subarctic regions of the Nearctic Region. North American localities are mapped in Fig. 171.

Collecting notes.— Lindroth (1945, 1961) described the habitat of Scandinavian specimens under *E. riparius.* North American specimens were found almost exclusively along large subarctic rivers on silt beaches south of the tree line, specifically in front of the willow zone where a dense carpet of *Equisetum fluviatile* grew. Specimens of this species of horsetail have few short side branches, thus leaving the silt beach mostly sun-exposed. Adults were not found on sun-exposed silt substrate inside the willows. I found numerous specimens on silt and organic beaches of a small water reservoir with artificially depressed water table. At this reservoir, *E. americanus* also occurred though more abundantly on organic beaches. This last species was not found near the river.

Taxonomic notes.— Adults of this species are very similar to those of *E. riparius.* The reasons for keeping both taxa specifically distinct are discussed under *E. riparius.* Based on description of adults and their type locality the following nominal forms are probably conspecific with *E. tuberculatus: E. latipennis, E. latipennis* ab. *costulifer* and *E. tumidiceps.* I did not find the original description of *E. latipennis* ab. *normalis,* but Semenov associated it with *E. tuberculatus. E. latipennis* var. *orientalis*, based on the description of puncture density, may be *E. riparius* or the North American *E. tuberculatus* (the type locality along the lower Lena River is reminescent of the North American situation). Based on descriptions of the type series and on type localities of *E. violaceomaculatus* and *E. dilaticollis,* both in subarctic or arctic regions of the Pacific coast of Asia, these forms may belong to this species rather than to *E. riparius* as suggested by Semenov (1895) who saw original specimens of these species.

Table 39. Descriptive statistics for *E. parviceps*, based on ten males and ten females from Anderson River Delta, N.W.T.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.30–1.55	1.46	0.088	0.026	4.0
PW	1.37–1.77	1.61	0.145	0.043	6.0
EL	3.65–4.40	4.13	0.298	0.078	4.2
EW	1.42–1.60	1.53	0.070	0.021	3.0
HW	1.60–1.75	1.69	0.061	0.018	2.4
B. Proportions					
PL/PW	0.824–1.127	0.912	0.091	0.028	6.7
PL/EL	0.333–0.390	0.354	0.019	0.006	3.7
PL/EW	0.912–1.069	0.959	0.054	0.016	3.7
PL/HW	0.812–0.939	0.864	0.043	0.012	3.3
PW/EL	0.346–0.420	0.390	0.027	0.008	4.6
PW/EW	0.948–1.136	1.054	0.072	0.022	4.6
PW/HW	0.833–1.000	0.950	0.067	0.020	4.7
EL/EW	2.561–2.767	2.707	0.081	0.024	2.0
EL/HW	2.280–2.559	2.438	0.097	0.030	2.7
EW/HW	0.870–0.926	0.901	0.025	0.008	1.9

Elaphrus parviceps Van Dyke

Figs. 4, 12, 116, 129, 136, 142, 144, 171

Elaphrus parviceps Van Dyke, 1925:112. Type locality: Seward Penninsula, Alaska; type (seen by me) in California Academy of Sciences, San Francisco. Lindroth, 1961:116.
Elaphrus riparius; Lindroth, 1961:116 *(ex parte) nec* Linnaeus, 1758.
Elaphrus americanus; Judd, 1967:51 *nec* Dejean, 181.

Adults

Diagnostic combination.— Separated from adults of most species by fewer punctures on each side of the abdominal sternum 3 (0 to 50). Similar to those of *E. tibetanus,* but separated by short sinuation on pronotum and large punctures in elytral pits (25 to 30 microns in diameter).

Description.— Two color forms. For details see *E. lecontei* (p. 295) except tibiae metallic on dorsal surface.

Antennomere 3 with 10 to 20 accessory setae. Frons without medial impression or accessory setae. Pronotum with lateral margin slightly convex, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25 and 77d); disc with or without one pair of indistinctly outlined submedial impressions and, in most specimens, with accessory setae. Abdominal sterna in both sexes with abundant accessory setae extended laterally to edge of sterna 5 and 6. Main mirror of elytron rectangular; mirrors sharply outlined in first two or three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

Integument sculpture. Punctures 25 to 30 microns in diameter on elytral intervals, 30 microns in diameter in pits, 25 microns in diameter on head and pronotum, and 30 to 35 microns in diameter on proepisternum. Punctures 10 to 20 microns apart in elytral pits, 20 to 30 microns apart on intervals 4, 6 and 8, 10 to 30 microns apart submedially and 40 to 60 microns apart antero-laterally on pronotum, and 30 to 40 microns apart on proepisternum. First sutural pit of elytron with three to five concentric rows of punctures. Abdominal sternum 3 with 0 to 50 punctures (usually 20 or less).

Microsculpture granulate in elytral pits, granulate to subconvex dorsally, convex to subconvex on thoracic pleura and flat on abdominal sterna (surface quite brilliant).

Male genitalia. As in *E. riparius* (Figs. 61a, 61b, 69c).

Measurements and proportions.— Four samples studied, and data for one presented in Table 39.

Variation.— Specimens from Alaska have a brighter surface and sparser punctures than those east of Alaska. Otherwise, no other differences were observed between above samples.

Distribution.— Known along southern arctic regions from the western shore of Hudson Bay to Commander Islands (U.S.S.R.). North American localities are mapped in Fig. 171.

Collecting notes.— Adults were found commonly on shores of small lakes and ponds, but not along shores of rivers, though these ponds were close to rivers (Ball pers. comm.).

Taxonomic notes.— I examined about 250 specimens, and dissected six males. The presence of this species on the Commander Islands suggests almost certainly its presence on Kamchatka and easternmost Siberia. Therefore, possibly the names *E. dilaticollis* and *E. violaceomaculatus,* synonymized under *E. riparius* by Semenov, (1895) may refer to this species.

Geographical affinities.— The range of *E. parviceps* is adjacent to ranges of the related species *E. americanus* and *E. tuberculatus.* Only few specimens of *E. parviceps* were found in the range of the latter two species.

Elaphrus tibetanus Semenov

Elaphrus tibetanus Semenov, 1904a:22. Type area: Eastern Tibet, China, type not seen but specimens from original series seen.

Adults

Diagnostic combination.— Similar to adults of *E. parviceps*, and distinguished as follows: pronotum with longer sinuation, punctures small (20 microns in diameter) in elytral pits and large (25 microns in diameter) on pronotum.

Description.— Two color forms: green and copper. For details see *E. lecontei* (p. 295) except tibiae metallic on dorsal surface.

Antennomere 3 with 10 to 20 accessory setae. Frons without medial impression and accessory setae. Pronotum with lateral margin slightly convex and elongate, obliterated and not beaded in sinuation, and not explanate before sinuation (Figs. 25, 77d); disc without or with one pair of indistinctly outlined submedial impressions, and with accessory setae in most specimens. Abdominal sterna of both sexes with abundant accessory setae extended laterally in punctate area. Main mirror of elytron rectangular; mirrors sharply outlined in first two or three rows. Elytral pits moderately wide (intervals 4, 6 and 8 quite straight) and very slightly impressed. Dorso-subapical surface of hind femur with one to three short (40 microns) setae (Fig. 34).

Integument sculpture. Punctures 20 microns in diameter in elytral pits, 25 microns in diameter or pronotum, and 30 microns in diameter on proepisternum. Punctures 20 to 30 microns apart in elytral pits, 10 to 20 microns apart in intervals 4, 6 and 8 and on pronotum submedially, 40 microns apart antero-laterally on pronotum, and 20 to 30 microns apart on proepisternum.

Microsculpture granulate on most of dorsal surface, convex on thoracic pleura, and flat on abdominal sterna (surface brilliant).

Male genitalia. Median lobe not associated with dissected male. Palmén (1944:21) figured the lobe in lateral aspect; the apex seems shorter and wider than in *E. riparius,* and setae of paramere seem short.

Measurements and proportions.— Based on two specimens from the Basin of the Yellow River, China. PL, 1.3-1.3 mm; PW, 1.4-1.6 mm; EL, 3.4-3.5 mm; EW, 1.2-1.4 mm; HW, 1.4-1.6 mm; PL/PW, 0.84-0.91; PL/EL, 0.37-0.39; PL/EW, 0.95-1.08; PL/HW, 0.82-0.91; PW/EL, 0.42-0.44; PW/EW, 1.12-1.18; PW/HW, 0.97-1.00; EL/EW, 2.56-2.80; EL/HW. 2.21-2.36; EW/HW, 0.84-0.86.

Variation.— Only two adults studied, thus not discussed.

Distribution.— Known from eastern Chinese highlands; for details see Semenov (1904a). I have seen two adults out of 55 seen by Semenov from the valley of Dzatshu River and Sergtshu in the Yellow River Basin.

Collecting notes.— Collected by the Koslov expedition from late April to July 1901 at various proximate locations between 11,000′and 14,000′(Russian feet) above sea level.

Geographical affinities.— The present range of this species does not overlap those of other species.

SPECIES OF UNKNOWN STATUS

Elaphrus smaragdiceps Semenov

Elaphrus smaragdiceps Semenov 1889:354. Type locality: Dshoni (8,820 ') in Amdo Mountains, Kansu, China; type not seen. Semenov 1904a:19. 1904b:125.

Taxonomic notes.— The type series belongs to subgenus *Elaphrus* as the prosternum is pubescent and only the three basal tarsomeres of forelegs of males have spongy pubescence (Semenov, 1904a).

The following character combination suggests that Semenov's species is probably distinct. I cannot include it in my key as many important characters were not observed by Semenov. The following characters were judged potentially more significant: pronotum longer than wide, lateral margin slightly convex and sinuation elongate; lateral margin of elytra markedly constricted in basal 0.3, only mirrors in first row clearly outlined; tibiae red-brown, but metallic at base and apex.

The male seems to have elytra as in adults of *E. californicus,* and body features like those of *E. ulrichi.* The color peculiarities (bright green head and pronotum and copper elytra) may be aberrant as suggested by Semenov (1904): "*capite majore ex parte smaragdino-viridi, semperne?*", though it matches that of the bicolor form of *E. californicus.* Among known Palaearctic species, the male of this species is the only one with very constricted elytra. Lindroth (1961) illustrates the constriction of *E. californicus* in Fig. 57b. Other characteristics, though interesting, are variable, and should be used with care.

Elaphrus irregularis Scudder

Elaphrus irregularis Scudder, 1890. Type locality: Scarborough, Toronto, Ontario; type seen in the Museum of Comparative Zoology, Cambridge, Massachusetts.

Taxonomic notes.— The fossil elytron is in poor condition. However, sculpture, mirrors and pits clearly associate the type with members of subgenus *Elaphrus.* It is not *E. ruscarius* (larger elytral punctures than those on the fossil), nor *E. californicus* (denser punctures on elytra than those on the fossil), nor *E. tuberculatus* of North America (mirrors with some meshes of microsculpture, absent from the fossil). Character states on fossils match either *E. americanus* or *E. parviceps,* being in the range of overlap between these two species. The following combination of characters would suggest a match with *E. parviceps:* punctures spaced in elytral pits near main mirror (two or three microsculpture meshes between punctures), and in interval 1 and 2; punctures generally large (30 microns in diameter) in elytral pits near main mirror, and on intervals 1 and 2; microsculpture convex over most of surface except on mirrors. Since the type is in poor condition, and *E. parviceps* and *E.*

americanus are known from fossil samples at the type locality, I prefer to leave *E. irregularis* as incertae sedis.

Subgenus *Elaphroterus* Semenov

Elaphroterus Semenov, 1895:309, 313. Type-species: *Elaphrus aureus* Müller, 1821, fixed by Semenov (1926), by subsequent designation. Semenov, 1904a:19 *(ex parte)*. Jacobson, 1906:267 *(ex parte)*. Reitter, 1908:96, 97 *(ex parte)*. 1909:104 *(ex parte)*. Bänninger, 1919: 149 *(ex parte)*. Porta, 1923:78 *(ex parte)*. Semenov, 1926:39. Portevin, 1929:41 *(ex parte)*. Jeannel, 1941:216. Hatch, 1953:63. Ball, 1960:106. Lindroth, 1961:119. Nakane, 1963:19.

Elaphrotatus Semenov, 1895:308. Type-species: *Elaphrus punctatus* Motschulsky, 1846, fixed by Semenov (1926), by subsequent designation. Jacobson, 1906:268. Semenov, 1926:39. NEW SYNONYM.

Adults

Diagnostic combination.— Distinguished from adults of other subgenera as in following. Fringe of setae along posterior margin of pronotum extended to hind angles. Disc of prosternum and process of mesosternum asetose. Trochanter of foreleg with two setae. Trochanter of midleg with one or two setae. Setae on inner 0.5 of hind coxa.

Description.— *Head.* Frons without medial impression, Clypeus with one pair of setae. Terebral margin of right mandible more than 0.5 as long as mandible; basal retinacular tooth entire, and apex of retinacular tooth near terebral tooth. Maxillary palpomere 3, 0.3 length of palpomere 4. Galeomere 1, 1.5 length of maxillary palpomere 2.

Thorax. Lateral margin of pronotum beaded except in sinuation, or unbeaded. Fringe of setae along posterior margins of pronotum extended to hind angles; setae scimitar-shaped and moderately expanded apically. Prosternum without setae or with a few setae on prosternal process. Mesosternal process without setae; postero-lateral ridge of mesosternum absent.

Abdomen. Tergum 7 without setae except on stridulatory scraper plates.

Elytra. Striae lacking. Transverse basal stria indistinctly outlined at shoulder. Setigerous punctures of elytra 40 to 50 microns in diameter. Interval 3 with one to three wide mirrors (Fig. 116). Elytral pits with 25 punctures or more, punctures regularly distributed (Figs. 124, 125).

Legs. Foreleg: trochanter with two setae: femur with 35 to 50 setae; tibia with 17 to 27 setae; inner dorsal fringe of setae 0.7 as long as tibia, and without setae posteriorly; first three tarsomeres of males with spongy pubescence ventrally, or pubescence lacking. Midleg: trochanter with one or two setae; femur with 35 to 50 setae; tibia with about 70 setae. Hindleg coxa with three to 20 setae on inner half. Femur with 18 to 21 setae; tibia with 65 to 80 setae.

Male genitalia. Internal sac of median lobe without large scales basally.

Ovipositor. Basal sclerite of stylus without apico-ventral setae; apical sclerite without setae (Fig. 74).

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other subgenera as in following. Seta EA-E on frontale small. Epicranial suture 0.7 or less as long as antennal scape. Outer surface of stipes with membranous declivity behind postero-lateral seta, outer margin projected outward at declivity; postero-ventral pores proximate (Fig. 83b).

First Instar Larvae

Description.— Medial point of nasale acute; teeth of nasale slightly coarser than in larvae of subgenus *Elaphrus* , and ending at base of medial point (Fig. 92). Seta EA-E of frontale small. Epicranial suture less than 0.7 as long as antennal scape. Head short: bisinuation of lateral margin behind eye with anterior and posterior convexity subequal. Angle formed by seta DI-A and pores DI-P and DMP-E on parietale 90° to 110°. Triangle formed by setae DEP, VEM-P and VEP-P on parietale short (anterior angle open). Pointed microsculpture on 2 to 25% of ventral surface of parietale. Stipes with membranous declivity on ventral surface behind postero-lateral seta; lateral margin of stipes projected outward; dorsal surface of stipes with 40 to 50 setae on inner half, subapical setae roughly distributed in two to five rows; postero-ventral pores of stipes proximate (Fig. 83b). Pronotum with meshed microsculpture on 60% of surface, pointed microsculpture lacking. Pointed microsculpture on entire surface of anterior band of terga 1 to 8.

Second Instar Larvae

Description.— Outer margin of stipes behind postero-lateral seta protruded. Each sclerite of pronotum and of mesonotum with 20 to 40 accessory setae; pointed microsculpture on entire anterior band surface. Each sclerite of terga 1 to 8 with 16 to 28 accessory setae. Basal accessory seta of urogomphus dorso-medially; pointed microsculpture on entire anterior band of terga 1 to 9, and on entire posterior band of terga 1 to 8. Hypopleuron of segments 1 to 8 with about four accessory setae.

Third Instar Larvae

Description.— Surface of proepisternum with 10 accessory setae. Each sclerite of mesonotum with 30 to 55 accessory setae, mesonotal epipleuron with one to five accessory setae. Mesepimeron with two accessory pores or less. Largest projection of urogomphus in lateral view suggested or small. Sclerites of terga 1 to 8 each with 40 to 55 accessory setae. Epipleuron of abdominal segments 2 to 8 with 17 to 40 accessory setae. Hypopleuron of abdominal segments 1 to 8 with 12 to 22 accessory setae. Sternite of segment 1 with 14 to 18 accessory setae, that of segments 2 to 7 each with 25 to 40, that of segment 8 with 25 to 40, that of segment 9 with four to 12, and that of segment 10 with five to 12. Inner poststernites with two to five accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— The range of species of this subgenus extends across the Palaearctic Region and the western portion of the Nearctic Region, from the subarctic to the warm temperate zone.

Key to the species and subspecies of subgenus *Elaphroterus* Semenov

Adults

1 Dorsal surface with faint brassy hue. Punctures of pronotum 45 microns in diameter. Trochanter of midleg with two setae. Eastern Asia ..... *E. punctatus* Motschulsky p. 326

1′ Dorsal surface metallic green, gray-green or copper. Punctures of pronotum 30 microns in diameter. Trochanter of midleg with one seta 2

2 (1′) Lateral margin of pronotum beaded, bead extended along most of margin except in sinuation. Intercoxal process of prosternum of many specimens with one or two accessory setae. Cold temperate regions of Europe, isolated in Caucasus Mountains ..... *E. aureus* Müller p. 328

2′ Lateral margin of pronotum rounded, angular or barely beaded at middle. Intercoxal process of prosternum without accessory setae 3

3 (2′) Lateral margin of pronotum rounded or barely angulate near middle (Fig. 27). Femur testaceous, except for two metallic green spots, one medially and one apically. Tibia of foreleg of male with large sharp projection at base of posterior spur --best seen in posterior view of tibia (Fig. 149). Western Nearctic Region ..... *E. purpurans* Hausen p. 330

3′ Lateral margin of pronotum angular to great extent (Fig. 26). Femur red-brown or piceus except for metallic green dorsal surface. Tibia of foreleg of male without projection at base of posterior spur. Palaearctic or northwestern Nearctic Regions 4

4 (3′) Pronotum with many bright copper reflecting surfaces. Dorsal body surface bright due to lack of, or presence of flat microsculpture. Hind angle of pronotum without proximal setigerous puncture. Dorsal surface of head,

pronotum and side of elytron brilliant metallic golden-green. Elytron with one or two rows of indistinctly outlined mirrors. Accessory setae absent from posterior surface of metasternum. Middle Europe ..... *E. ulrichi* Redtenbacher p. 338

4′ Pronotum, at most, with dark copper reflecting surfaces. Dorsal body surface dull, due to convex microsculpture. Hind angle of pronotum with proximal setigerous puncture. Dorsal surface dull green, grey-green, bluish green, or copper. Elytron with three rows of distinctly outlined mirrors (Fig. 116). Accessory setae on posterior surface of metasternum. Boreal and subarctic regions of Palaearctic and Nearctic Regions 5

5 (4′) Dorsal surface of elytron relatively smooth: pits little impressed and mirrors flat. Punctures in intervals 4, 6 and 8, in most specimens 30 to 40 microns apart. Pronotum without accessory setae. Coxa of hind legs with two to five accessory setae. Metasternum without accessory setae laterally. Abdominal sterna 4, 5 and 6 with one to eight accessory setae. Color: bluish-gray dorsally with green legs. West of Yenisey River ..... *E. angusticollis longicollis* Sahlberg p. 336

5′ Dorsal surface of elytron relatively coarse: pits more deeply impressed and mirrors convex (Fig. 116). Punctures on intervals 4, 6 and 8, in most speciments 10 to 20 microns apart (Fig. 125). Pronotum of 50% of specimens with accessory setae. Coxa of hind leg with 10 to 20 setae. Metasternum with many accessory setae laterally. Abdominal sterna 4, 5 and 6 with 10 to 20 accessory setae. Color: green dorsally with green legs, or gray-green dorsally with copper femur and clypeus, or red-copper dorsally except for gray-green sutural and apical area of elytra. East of Lena River and in Northwestern portion of Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334

First Instar Larvae.

1 Epicranial suture short: 0.25 as long as antennomere 1. Apical inner margin of mandible and posterior edge of retinaculum distinctly toothed. Pointed microsculpture absent from latero-ventral surface of parietale. Europe ..... *E. aureus* Müller p. 328

1′ Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Apical inner margin of mandible and posterior margin of retinaculum smooth or indistinctly toothed. Pointed microsculpture on 5% or more of latero-ventral surface of parietale 2

2 (1) Seta MP and EM-P of frontale barely suggested or absent. Pointed microsculpture of parietale restricted latero-ventrally (5% of surface), and absent latero-dorsally Western Nearctic Region. ..... *E. purpurans* Hausen p. 330

2′ Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread latero-ventrally (20% or more of surface) and latero-dorsally (10% or more of surface) 3

3 (2′) Parietale dark brown only near frontale and epicranial suture.

Microsculpture of abdominal terga single-pointed. Pointed microsculpture well developed near sutural portion of mesonotum and metanotum. East of Lena River and in western Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334

3′ Parietale dark brown except behind eyes and along base. Microsculpture of abdominal terga multi-pointed. Pointed microsculpture absent from sutural portion of mesonotum and metanotum. Middle Europe ..... *E. ulrichi* Redtenbacher p. 338

Second Instar Larvae

1 Epicranial suture short: 0.25 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 20 accessory setae. Pointed microsculpture absent from parietale baso-laterally. Europe ..... *E. aureus* Müller p. 328

1′ Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 40 accessory setae. Pointed microsculpture well developed on parietale baso-laterally 2

2 (1′) Seta MP and EM-P of frontale absent. Pointed microsculpture of parietale restricted to latero-ventral portion (5% of ventral surface). Urogomphus, with only medium-sized and large accessory setae. Main accessory setae of hypopleura 1 to 8 large. Western Nearctic Region ..... *E. purpurans* Hausen p. 330

2′ Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread on latero-ventral portion (15% or more of ventral surface). Urogomphus, in addition to medium-sized and large accessory setae, with numerous very small ones. Main accessory setae of hypopleura 1 to 8 small 3

3 (2′) Parietale dark brown only near frontale and epicranial sutures; nota and terga brown. Microsculpture of abdominal terga single-pointed. Largest projection of urogomphus clearly outlined (Fig. 101a). East of Lena River and in western portion of Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334

3′ Parietale dark brown except behind eyes and along base; pronotum, tergum 1 and outer third of terga 2 to 8 red-brown, and mesonotum, metanotum and inner two thirds of terga 2 to 8 and tergum 9 dark brown. Microsculpture of abdominal terga multi-pointed. Largest projection of urogomphus in lateral view no more than barely outlined. Middle Europe ..... *E. ulrichi* Redtenbacher p. 338

Third Instar Larvae.

1 Epicranial suture short: 0.25 as long as antennomere 1. Each sclerite of mesonotum and metanotum with about 30 accessory setae. Pointed microsculpture of parietale absent laterally. Europe ..... *E. aureus* Müller p. 328

1′ Epicranial suture long: 0.4 to 0.5 as long as antennomere 1. Each sclerite of mesonotum and metanotum with 50 or more accessory setae. Pointed microsculpture of parietale well developed laterally 2

2 (1′) Setae MP and EM-P of frontale absent. Pointed microsculpture of parietale restricted to latero-ventral portion (5% of surface). Urogomphus with only medium-sized and large accessory setae. Main accessory setae on hypopleura 1 to 8 large. Lateral band of pronotum without microsculpture. Western Nearctic Region ..... *E. purpurans* Hausen p. 330

2′ Setae MP and EM-P of frontale present and very small. Pointed microsculpture of parietale widespread on latero-ventral portion (15% or more of surface). Urogomphus with numerous very small accessory setae in addition to medium-sized and large ones. Main accessory setae on hypopleura 1 to 8 small. Lateral band of pronotum with pointed microsculpture 3

3 (2′) Parietale dark brown only near frontale and epicranial suture; nota and terga dark brown. Microsculpture of abdominal terga single-pointed. Largest projection of urogomphus in lateral view about 0.5 as wide as urogomphus below. East of Lena River and in western portion of Nearctic Region ..... *E. angusticollis angusticollis* Sahlberg p. 334

3′ Parietale dark brown except behind eyes and along base; pronotum, tergum 1 and outer 0.3 of terga 2 to 8 red-brown, and mesonotum, inner 0.7 of terga 2 to 8 and tergum 9 dark brown. Microsculpture of abdominal terga multi-pointed. Largest projection of urogomphus in lateral view no more than barely outlined. Middle Europe .... *E. ulrichi* Redtenbacher p. 338

Elaphrus punctatus Motschulsky
Figs. 53a-c, 54a-b, 112, 124

Elaphrus punctatus Motschulsky, 1846:73. Type locality: Lake Baikal USSR; type not seen. Sahlberg, 1880:10. Marseul, 1882:4. 1881:67. Jacobson, 1906:268. Nakane, 1955:22. Nakane *et al.*, 1963:19. Ohkura, 1973:6.

Elaphrus cribratus Semenov, 1889:353. Type locality: China, Szetschuan in mountains of Amdo, 6000′; type not seen. Jacobson, 1906:268. (suggested synonym).

Adults

Diagnostic combination.— Distinguished from adults of other species by large punctures (30 to 60 microns), by almost black dorsal surface of body with weak metallic reflections, and by presence of four to six accessory setae on prosternal process and of two setae on trochanter of midleg.

Description.— Dorsal and ventral surfaces almost black with very weak green and copper reflections. Legs and mouthparts dark brown with weak metallic green reflections.

Antennomere 4 densely pubescent in apical 0.5. Pronotum with lateral margin very thinly and apparently completely beaded, with setigerous puncture near hind angle, and with one pair of submedial impressions. Prosternal process with four to six accessory setae. Accessory setae of metasternum present anteriorly, posteriorly and laterally. Abdominal sterna 4, 5 and 6 with more than ten accessory setae. Elytral mirrors flat, in three rows; sutural mirrors subequal in width. Elytral pits not impressed and not sharply outlined. Males without secondary sexual characters (first three tarsomeres of foreleg without spongy pubescence, tarsomeres narrow, and tibia of midleg without projection at base of inner spur). Trochanter of midleg with two setae, and coxa of hindleg with about 15 accessory setae. Tibia of foreleg without projection at base of posterior spur.

Integument sculpture. Punctures 30 microns in diameter on elytral intervals 4, 6 and 8, 40 to 50 microns in diameter on head, pronotum and elytral pits, and 50 to 60 microns in diameter ventrally. Punctures 10 to 20 microns apart

Table 40. Descriptive statistics for *E. punctatus*, based on six males and three females from USSR (Irkutsk), Japan (Ibaragi, Pref., Sairama), and China (northern China, Kuku–nor).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.32–1.57	1.50	0.121	0.054	5.3
PW	1.40–1.72	1.58	0.155	0.069	6.5
EL	3.30–4.02	3.70	0.372	0.165	6.7
EW	1.22–1.70	1.38	0.216	0.096	10.4
HW	1.67–1.95	1.82	0.130	0.058	4.7
B. Proportions					
PL/PW	0.912–0.999	0.952	0.043	0.020	3.0
PL/EL	0.385–0.449	0.407	0.028	0.012	4.7
PL/EW	0.779–1.224	1.098	0.199	0.088	12.1
PL/HW	0.791–0.873	0.826	0.037	0.016	3.0
PW/EL	0.404–0.464	0.427	0.025	0.012	4.0
PW/EW	0.824–1.255	1.153	0.195	0.086	11.3
PW/HW	0.836–0.901	0.868	0.033	0.014	2.5
EL/EW	1.941–2.980	2.700	0.442	0.196	10.9
EL/HW	1.944–2.137	2.034	0.087	0.038	2.8
EW/HW	0.690–1.015	0.762	0.147	0.066	12.9

submedially; 20 to 30 microns apart laterally on pronotum and 20 microns apart on elytral intervals 4, 6 and 8.

Microsculpture over most of dorsal body surface except of frons and elytral mirrors, more convex in elytral pits, and subconvex elsewhere; microsculpture of ventral body surface weakly outlined on most of abdominal sterna, elsewhere flat or absent in spots.

Male genitalia. Apex of median lobe in ventral view thin-edged and strongly twisted (Fig. 54a), and in lateral view short and subtruncate (Fig. 53a and 54b). Setae of parameres long (Fig. 53c).

Measurements and proportions.— One sample studied. See Table 40.

Variation.— Despite a small sample from a large area, I observed striking structural differences. Specimens from Lake Baikal, USR and Kuku-nor, China (Tibet) have indistinctly outlined and contrasted mirrors on elytron against the bright intervals 4, 6 and 8 (microsculpture absent or barely suggested, and punctures irregularly distributed on these intervals. However, specimens from Japan and Northern China have sharply outlined and contrasted mirrors against dull intervals 4, 6 and 8 (microsculpture subconvex, and regularly distributed on these intervals).

Distribution.— I have seen specimens from Irkustk (near Lake Baikal), USSR; Kuku-nor, 3200 m, China (Tibetan region); northern China; Honshu and Hokaido Islands, Japan.

Taxonomic notes.— The descriptions of *E. cribatus* and *E. punctatus* are similar and match available specimens. The specimens from Lake Baikal and Kuku-nor are near the type locality of each taxon. Since adults from these two localities are similar, I feel these two names refer to one form of one species.

I studied nine specimens and dissected two males.

Geographical affinities.— The range of this species is isolated from any other species of this subgenus.

Table 41. Descriptive statistics for *E. aureus*, based on ten males and ten females from Austria (Graz, Wien) and Switzerland.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.52–1.77	1.61	0.108	0.032	4.5
PW	1.62–1.90	1.74	0.109	0.033	4.2
EL	3.65–4.15	4.00	0.211	0.063	3.6
EW	1.40–1.60	1.49	0.085	0.026	3.8
HW	1.67–2.07	1.96	0.098	0.029	3.3
B. Proportions					
PL/PW	0.886–0.972	0.952	0.036	0.010	2.6
PL/EL	0.387–0.428	0.409	0.018	0.006	2.9
PL/EW	1.033–1.143	1.084	0.039	0.012	2.4
PL/HW	0.787–0.855	0.820	0.028	0.008	2.3
PW/EL	0.419–0.466	0.441	0.021	0.006	3.2
PW/EW	1.117–1.232	1.170	0.048	0.014	2.7
PW/HW	0.848–0.916	0.885	0.031	0.010	2.4
EL/EW	2.594–2.733	2.654	0.057	0.016	1.4
EL/HW	1.921–2.078	2.009	0.061	0.018	2.0
EW/HW	0.737–0.779	0.757	0.019	0.006	1.7

Elaphrus aureus Müller

Figs. 55a-c, 101a-b

Elaphrus aureus Müller, 1821:229. Type locality: not given; type not seen. Herr, 1838:39. Motschulsky, 1846:72. Küster, 1846:7. Letzner, 1849:52. Chaudoir, 1850:161. Fairmaire and Laboulbène 1854:6. Schaum, 1856:74. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Fauvel, 1882:82, 84. Marseul, 1882:4. Reitter, 1887:16. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:305. 1897:596. Everts, 1898:49. Jacobson, 1906:267. Semenov, 1907:259. Reitter, 1908:96, 97. 1909:106. Kuhnt, 1912:50. Fairmaire, 1913:31. Schaufuss, 1916:29. Bänninger, 1919:149. Porta, 1923:78. Semenov, 1926:40. Portevin, 1929:41. Jeannel, 1941:217.

Elaphrus littoralis Dejean, 1826:275. Type area: Ukraine, Hungary and Austria; type not seen. Erichson, 1837:4. Heer, 1838:39. Motschulsky, 1846:73. Küster, 1846:7. Letzner, 1849:52. Chaudoir, 1850:161. Fairmaire and Laboulbène 1854:6. Schaum, 1856:74. Stierlin, 1869:11. Marseul, 1882:4. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Everts, 1898:49. Jacobson, 1906:267. Bänninger, 1919:149. Jeannel, 1941:217.

Elaphrus smaragdinus Reitter, 1887:16. Type locality: Czechoslovakia, near Paskov on shore of Ostravice River; type not seen. Ganglbauer, 1892:123, 124. Semenov, 1895:306. Gerhardt, 1899:14. Semenov, 1907:259.

Elaphrus smaragdinus; Jacobson, 1906:267.

Elaphrus tschitscherini Semenov, 1897:595. Type area: Caucasus, USSR: type not seen. Jacobson, 1906:268.

Elaphrus aureus var. *smaragdinus;* Reitter, 1908:96, 97. 1909: 106. Kuhnt, 1912:50. Schaufuss, 1916:29.

Elaphrus tchitcherini; Semenov, 1926:40 (invalid emendation).

Adults

Diagnostic combination.— Distinguished by beaded lateral margin of pronotum from other metallic species of this subgenus.

Description.— Dorsal surface gray-green. Microsculptured surfaces brass or weakly copper colored; punctures green or blue-green; elytral pits purple near setigerous puncture. Femur dark brown underneath and metallic above.

Table 42. Descriptive statistics for *E. aureus*, based on five males and three females from Caucasus Mountains, USSR (Taberda, Kislovodsk).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.37–1.57	1.52	0.099	0.047	4.3
PW	1.57–1.75	1.65	0.094	0.044	3.8
EL	3.75–4.10	3.88	0.195	0.092	3.3
EW	1.30–1.50	1.42	0.110	0.052	5.2
HW	1.77–1.97	1.88	0.112	0.053	3.9
B. Proportions					
PL/PW	0.846–0.954	0.919	0.055	0.026	4.0
PL/EL	0.367–0.406	0.392	0.018	0.008	3.1
PL/EW	1.033–1.154	1.071	0.060	0.028	3.7
PL/HW	0.775–0.833	0.808	0.028	0.014	2.4
PW/EL	0.417–0.439	0.426	0.013	0.006	2.1
PW/EW	1.121–1.226	1.166	0.060	0.028	3.4
PW/HW	0.844–0.915	0.879	0.030	0.014	2.4
EL/EW	2.632–2.885	2.735	0.126	0.060	3.1
EL/HW	1.987–2.130	2.062	0.072	0.034	2.3
EW/HW	0.722–0.781	0.754	0.030	0.014	2.8

Antennomere 4 densely pubescent in apical 0.5. Pronotum with lateral margin clearly beaded except in sinuation, with setigerous puncture near hind angle of pronotum, and with one pair of submedial impressions. Prosternal process with fewer than three accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal sterna 4, 5 and 6 with three to six accessory setae. Elytral mirrors in two rows, clearly outlined, and convex; first or first and third sutural mirrors wider. Elytral pits not impressed and weakly outlined. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

Integument sculpture. Punctures 30 microns in diameter dorsally, but 15 to 20 microns in diameter on elytral intervals 4, 6 and 8, and 40 microns in diameter ventrally. Punctures 15 to 30 microns apart dorsally except antero-laterally on pronotum (30 to 40 microns apart) and in elytral pits (10 to 20 microns apart).

Microsculpture convex on dorsal and ventral surfaces, but flat on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view, thin-edged and straight (Fig. 55b), and in lateral view moderately long, round and wide (Fig. 55c). Setae of parameres long (Fig. 53c).

Measurements and proportions.— Three samples studied, data for two presented in Tables 41 and 42.

Variation.— Samples from Austria, Yugoslavia and Caucasus are very similar, but the mean of ratios PL/EL and PW/EL is significantly smaller for the Caucasus sample than for those of middle Europe. Thus, there is evidence that *E. tschitscherini* may represent a geographical race. However, larger samples are needed to clarify this problem.

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of subsequently described species by short epicranial suture (0.25 as long as antennomere 1), and restricted microsculpture on parietale (2% of latero-ventral surface).

Description.— Parietale dark brown dorsally but paler behind eyes and along base; nota and terga dark brown. Apical inner margin of mandible and posterior margin of retinaculum clearly toothed; retinaculum narrow (about 2.5

times wider than long). Setae MP and EM-P of frontale lacking, though puncture present. Epicranial suture 0.25 as long as antennomere 1. Parietale with microsculpture laterally (10% of latero-dorsal and 2% of latero-ventral surface), and without pointed microsculpture; mesonotum and metanotum without pointed microsculpture near suture. Microsculpture of terga single-pointed.

Second and Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by short epicranial suture (0.25 length of antennomere 1), and lack of microsculpture laterally on parietale.

Second Instar Larvae

Description.— Nota and terga dark brown. Parietale without microsculpture laterally, and pointed microsculpture. Each sclerite of pronotum with less than 30 accessory setae, and without microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A medium-sized; each sclerite with less than 20 accessory setae, and lateral band with one or two accessory setae; pointed microsculpture present laterally (15% of surface). Largest projection on urogomphus small in lateral view: 0.5 as long as width of urogomphus below. Each sclerite of terga 1 to 8 with about 15 accessory setae. Urogomphus without very small accessory setae. Base of tergum 10 with fine multi-pointed microsculpture. Abdominal epipleura 2 to 7 with five to seven accessory setae; microsculpture single-pointed. Abdominal hypopleura 2 to 7 with three to five accessory setae and some large. Membrane microsculpture consisting of fine points.

Third Instar Larvae

Description.— Parietale with microsculpture restricted dorso-laterally (less than 5% of surface), and without pointed microsculpture. Each sclerite of pronotum with about 30 accessory setae. Mesonotum and metanotum with pointed sculpture on lateral portions only (10% surface). Lateral band of terga 1 to 8 narrow, not enlarged posteriorly, and with less than 12 accessory seta; terga with about 30 accessory setae on each sclerite. Abdominal epipleuron 1 with eight to ten accessory setae, and epipleura 2 to 7 with about 20. Abdominal hypopleura 2 to 7 with about 15 accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— This is a middle European species ranging form Germany and Poland in the North, to France, the Northern shore of the Mediterranean, and Bulgaria in the South, but isolated in the Caucasus (Turin *et al.*, 1977). I have seen specimens from France, Germany, Poland, Yugoslavia, Czechoslovakia, Bulgaria, Austria and the Caucasus.

Taxonomic notes.— I have not seen Dejean's type of *E. littoralis,* but the description leaves no doubt as to the identity of his specimen with this species. The description of *E. smaragdinus* matches that of *E. aureus* except for greener surface (Semenov, 1907). Semenov (1897, 1926) recognized *E. tschitscherini* because of the isolated distribution of his type series relative to that of *E. aureus* and *E. angusticollis longicollis.* I have seen eight specimens from the Caucasus, and they match almost perfectly those of *E. aureus.* The Caucasus population may be a glacial relic.

I studied about 120 adults and dissected six males. I examined three first instar, two second instar and four third instar larvae from Austria.

Collecting notes.— Bauer (1976) collected adults on moist and bare soil along margins of rivers with moderate current near the forest zone. He did not specify if adults run on sun-exposed or shaded surfaces. However, adults of this and following species are found on upper beaches away from water.

Geographical affinities.— The ranges of this species and *E. ulrichi* overlap.

Elaphrus purpurans Hausen

Figs. 27, 56a-c, 74, 86, 92a-b, 102a-b, 173

Elaphrus pallipes Horn, 1878:51. Type area: Oregon and British Columbia; type (seen by me) in Museum of Comparative Zoology, Cambridge, Massachusetts. Junior homonym of *E. pallipes* Duftschmid 1812:197. (=*Asaphidion*

Table 43. Descriptive statistics for *E. purpurans*, based on ten males and ten females from Spring Creek Basin, Alberta.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.40–1.60	1.50	0.077	0.023	3.4
PW	1.49–1.60	1.53	0.080	0.024	3.5
EL	3.60–4.25	3.96	0.271	0.081	4.5
EW	1.32–1.52	1.45	0.078	0.023	3.6
HW	1.70–1.90	1.81	0.100	0.030	3.7
B. Proportions					
PL/PW	0.937–1.000	0.975	0.031	0.010	2.2
PL/EL	0.360–0.393	0.379	0.013	0.004	2.4
PL/EW	0.983–1.069	1.030	0.028	0.008	1.8
PL/HW	0.776–0.853	0.828	0.028	0.008	2.3
PW/EL	0.372–0.410	0.388	0.015	0.004	2.6
PW/EW	1.033–1.113	1.057	0.030	0.008	1.9
PW/HW	0.817–0.875	0.849	0.027	0.008	2.1
EL/EW	2.632–2.833	2.722	0.085	0.026	2.1
EL/HW	2.055–2.297	2.187	0.082	0.024	2.5
EW/HW	0.779–0.833	0.804	0.024	0.008	2.0

pallipes Duftschmid), discovered by Silverberg (1977). Schaupp, 1878:6. Austin, 1880:5. Wickham, 1893:202, 203. Keen, 1905:297. Van Dyke, 1924:3. Clark, 1948:25. Hatch, 1953:63. Lindroth 1961:119.

Elaphrus purpurans Hausen, 1891:251. Type area: British Columbia; type not seen. Hatch, 1953:11. Lindroth, 1961:119.

Adults

Diagnostic combination.— Distinguished from adults of other species by unbeaded lateral margin of pronotum, by presence of two distinct metallic green spots on dorsum of femur, and by projection at base of posterior spur of tibia of foreleg (much larger in males than in females).

Description.— Three distinct color forms. Gray-green form: microsculptured surface dark copper and punctures green or blue-green--areas with dense puncture gray-green and those with scattered punctures dark copper. Copper form: head and pronotum with punctures and microsculptured surfaces bright copper; elytra bright copper at base and along outer 0.5, remainder as in gray-green form. Dark form (absent east of Rockies): head, pronotum, inner 0.5 and apical 0.3 of elytra as in gray-green form; base and outer 0.5 of elytra with purple or dark blue punctures and microsculptured areas. Elytral pits purple near setigerous puncture. Femora with two metallic spots on dorsum.

Antennomere 4 pubescent in apical 0.5. Pronotum with lateral margin unbeaded with setigerous puncture near hind angle of pronotum, and with one pair of weakly outlined submedial impressions. Prosternal process without accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal sterna 4, 5 and 6 with 18 to 25 accessory setae. Elytral mirrors in two to three rows, sharply outlined, and slightly convex; sutural mirrors with first, or first and third mirrors wider. Elytral pits weakly outlined and not impressed. Secondary sexual characters of males typical of genus, but without projection at base of inner spur of tibia of midleg. Trochanter of midleg with one seta. Tibia of foreleg with projection present at base of posterior spur (much larger in males than in females).

Integument sculpture. Punctures 20 to 25 microns in diameter on elytron and head, 25 microns in diameter on pronotum, and 25 to 30 microns in diameter on ventral surface. Punctures 5 to 15 microns apart dorsally, but 5 microns apart in pits, and 50 to 70 microns apart antero-laterally on pronotum.

Table 44. Descriptive statistics for *E. purpurans*, based on nine males and 11 females from McMinnville, Oregon.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.65	1.50	0.085	0.025	3.8
PW	1.40–1.60	1.49	0.082	0.024	3.6
EL	3.40–3.90	3.67	0.201	0.060	3.6
EW	1.25–1.45	1.34	0.082	0.024	4.1
HW	1.72–1.92	1.81	0.079	0.024	2.9
B. Proportions					
PL/PW	0.950–1.071	1.011	0.048	0.014	3.2
PL/EL	0.387–0.446	0.412	0.021	0.006	3.4
PL/EW	1.071–1.200	1.122	0.048	0.016	3.2
PL/HW	0.792–0.870	0.835	0.031	0.010	2.5
PW/EL	0.390–0.432	0.407	0.015	0.004	2.5
PW/EW	1.071–1.154	1.110	0.033	0.010	2.0
PW/HW	0.800–0.863	0.826	0.025	0.008	3.1
EL/EW	2.643–2.808	2.727	0.059	0.018	1.4
EL/HW	1.943–2.113	2.029	0.074	0.022	2.4
EW/HW	0.714–0.768	0.744	0.028	0.008	2.6

Microsculpture of dorsal and ventral surfaces subconvex to convex, but subconvex to flat on abdominal sterna.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 56c), and in lateral view extremely wide and subtruncate (Fig. 56a). Setae of paramere short (Fig. 56b).

Measurements and proportions.— Six samples studied, and data for two presented in Tables 43 and 44.

Variation.— Samples across the range are rather similar. However, west of the Rockies, three color forms occur while only two are known to the east (dark form lacking). Also the largest projection of urogomphus of the second and third instar larvae is smaller east of the Rockies than west of them (based on one sample from coastal Oregon and a few samples from Alberta).

The variation between samples is clinal from Alberta and Alaska to California as shown by ratios PL/EW, PW/EL, EL/HW and EW/HW. However, two groups are suggested: one including samples from Alberta, Alaska and coastal Washington, and another including samples from south central British Columbia, Oregon and California. The northern group have significantly smaller means for ratio PL/EL, and larger means for ratio PW/HW than those of the southern group.

Because of limited number of samples, the data are not sufficient for conclusions. This preliminary information may be useful in future studies of infraspecific variation in this species.

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. aureus* by long epicranial suture, by smooth apical inner margin of mandible and posterior margin of retinaculum, and by

presence of pointed microsculpture dorso-laterally on parietale. Distinguished from subsequently described species by lack of setae MP and EM-P on frontale, and by restricted microsculpture latero-ventrally on parietale (5% of surface).

Description.— Parietale brown dorsally but paler behind eyes and base; nota and terga brown. Apical inner margin of mandible and posterior margin of retinaculum barely toothed or smooth; retinaculum normal (about 2 times wider than long). Setae MP and EM-P of frontale lacking, though punctures present. Epicranial suture 0.4 to 0.5 as long as antennomere 1. Parietale with microsculpture laterally (30% of dorsal and 5% of ventral surface), and without pointed microsculpture dorsally (5% of surface). Mesonotum (at base) and metanotum with pointed sculpture near suture. Microsculpture of abdominal terga single-pointed.

Second and third Instar Larvae

Diagnostic combination.— Distinguished from larvae of *E. aureus* by long epicranial suture, and by presence of some pointed sculpture laterally on parietale. Distinguished from subsequently described species by lack of very small accessory setae on urogomphus surface.

Second Instar Larvae

Description.— Nota and terga brown. Parietale with microsculpture restricted laterally (5% of ventral and dorsal surfaces), and with pointed microsculpture restricted laterally (3% of dorsal and 5% of ventral surfaces). Each sclerite of pronotum with about 35 accessory setae, and without microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A medium-sized; each sclerite with about 40 accessory setae, and lateral band with one or two accessory setae; pointed microsculpture widespread laterally (30% of disc surface) and at base near suture. Largest projection of urogomphus short in lateral view (0.3 to 0.5 as long as width of urogomphus below). Each sclerite of terga 1 to 8 with about 15 accessory setae. Urogomphus without very small accessory setae. Base of tergum 10 with fine multipointed microsculpture. Abdominal epipleura 2 to 7 with five to seven accessory setae; pointed microsculpture single-pointed. Abdominal hypopleura 2 to 7 with three to five accessory setae and some large. Membrane microsculpture consisting of fine points.

Third Instar Larvae

Description.— Parietale with microsculpture laterally (20% of dorsal and 5% of ventral surface), and with restricted pointed microsculpture laterally (5% of ventral surface). Each sclerite of pronotum with about 45 accessory setae. Mesonotum and metanotum with pointed microsculpture on lateral portion only (10 to 15% of surface). Lateral band of terga 1 to 8 narrow (not enlarged posteriorly) and with less than 12 accessory setae; terga 1 to 8 with about 35 accessory setae on each sclerite. Abdominal epipleuron 1 with eight to ten accessory setae, and epipleura 2 to 7 with about 20. Abdominal hypopleura 2 to 7 with about 15 accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— A western Nearctic species extending from forested regions of the Pacific coast (between Alaska and central California) east to Mackenzie River, Northwest Territories, Alberta, Idaho, and western Oregon and California (Fig. 173).

Taxonomic notes.— I have not seen the type of *E. purpurans* but the description clearly refers to the copper form of this species where, in British Columbia, (the type area), there is no other coppery colored *Elaphroterus*.

I studied about 1000 adults and dissected nine males. I examined six first instar, four second instar and three third instar larvae from Conjuring Creek, Alberta, and three third instar larvae from western Oregon.

Collecting notes.— Adults are less hygrophilous, run in the shade, and are found on upper beaches of rivers. The surface is bare or covered with leaf litter. The soil consists of sand, silt, or a mixture of both. The slope of the beaches varies from flat to almost vertical. Adults are found along rivers originating from mountains with summer melting period or for a few kilometers along adjoining creeks. I found adults along torrential glacial rivers where water levels may fluctuate as much as three meters a day, and along slow and warm creeks (Conjuring Creek,

Alberta) with moderate and irregular water level fluctuations. The life cycle is typical of the genus as outlined under *E. clairvillei*. I found only one larva on an upper beach. I do not know where adults overwinter.

Geographical affinities.— Sympatric with *E. angusticollis angusticollis* in subarctic regions.

Elaphrus angusticollis Sahlberg

Adults

Diagnostic combination.— Distinguished from adults of preceeding species by traceable but unbeaded lateral margin of pronotum, and from those of *E. ulrichi* by presence of setigerous puncture near hind angle of pronotum. Most similar to adults of *E. purpurans,* but separated on femora color: dark brown below and dark metallic green above (metallic spot not divided in two).

Variation.— Under this name, two distinct forms are recognized: one extending from northern Europe east to the Yenisey River, and another from the Lena River, in eastern Siberia, to the Pacific coast, and from Alaska east to the Mackenzie River. Adults of each form are distinguished by characters, described below, under each subspecies.

Similar groupings are clearly suggested following comparisons of means of many ratios between three samples. The ratio EL/HW between adults of *E. angusticollis angusticollis* and *E. angusticollis longicollis* is significantly and taxonomically different. Also samples of *E. angusticollis angusticollis* relative to those of the other subspecies show significantly larger means for ratios PW/EW, EL/EW and EW/HW, and smaller means for ratios PL/EL, PL/EW and PW/EL.

Because of marked differences in many structural and in one behavioural characters, the lack of clinal variation, and the allopatric distribution of these two forms, I feel they should be considered at least subspecifically distinct.

Elaphrus angusticollis angusticollis Sahlberg

Figs. 26, 58, 113, 125, 151, 152, 156, 173

Elaphrus angusticollis R.F. Sahlberg, 1844:20. Type locality: Ochota River near Ochotsk (eastern Siberia), USSR; type not seen. Sahlberg, 1880:11. Marseul, 1882:4. Semenov, 1904c:105. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

Elaphrus angustatus Chaudoir, 1850:161. Type area: Eastern Siberia; type not seen. Sahlberg, 1880:11. Marseul, 1882:4. Semenov, 1895:306. 1904c:104. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

Adults

Diagnostic combination.— Distinguished from adults of *E. angusticollis longicollis* as follows: elytral mirrors convex; punctures on elytral intervals 4, 6 and 8 denser (10 to 20 microns apart); many accessory setae on hind coxa (10 to 20), on side of metasternum (abundant), and on abdominal sterna 4, 5 and 6 (10 to 20).

Description.— Three color forms. Gray-green form: microsculptured surface dark copper and punctures green or blue-green dorsally; mouthparts and antennomere 1, 2 and 3 bright copper; femur golden or bright copper. Green form: microsculptured surface copper (usually brighter than gray-green form) and punctures green or blue-green dorsally; mouthparts, antennomere 1, 2 and 3, and femora bright green. Copper form: head, pronotum, base and outer 0.5 of elytra with bright copper microsculptured surfaces and punctures; inner 0.5 and apex of elytra as in gray-green form. Femora of all forms metallic on dorsum and not divided.

Antennomere 4 pubescent in apical 0.5. Pronotum with lateral margin unbeaded but traceable except in sinuation, with setigerous puncture near hind angle of pronotum, and with one pair of weakly outlined submedial impressions. Prosternal process without accessory setae. Accessory setae of metasternum present anteriorly and posteriorly. Abdominal

Table 45. Descriptive statistics for *E. angusticollis angusticollis*, based on ten males and ten females from Omsuktschan, USSR (eastern Siberia).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.40–1.57	1.48	0.082	0.024	3.7
PW	1.45–1.70	1.57	0.084	0.025	3.6
EL	3.90–4.40	4.15	0.218	0.065	3.5
EW	1.40–1.62	1.50	0.088	0.026	3.9
HW	1.70–1.90	1.79	0.076	0.023	2.8
B. Proportions					
PL/PW	0.882–0.984	0.939	0.045	0.014	3.2
PL/EL	0.341–0.367	0.356	0.012	0.004	2.0
PL/EW	0.923–1.034	0.986	0.045	0.014	3.0
PL/HW	0.781–0.863	0.824	0.034	0.010	2.8
PW/EL	0.366–0.400	0.379	0.017	0.006	2.9
PW/EW	0.985–1.086	1.050	0.043	0.012	2.8
PW/HW	0.833–0.944	0.877	0.033	0.010	2.5
EL/EW	2.667–2.900	2.772	0.094	0.028	2.3
EL/HW	2.192–2.411	2.317	0.095	0.028	2.7
EW/HW	0.789–0.890	0.836	0.042	0.012	3.3

sterna 4, 5 and 6 with 10 ro 20 accessory setae. Elytral mirrors in three rows, sharply outlined, and convex; first, or first and third sutural mirrors wider. Elytral pits weakly impressed and outlined. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

Integument sculpture. Punctures 20 to 25 microns in diameter dorsally. Punctures 10 to 20 microns apart dorsally, but 5 to 10 microns apart in pits and 40 to 50 microns apart antero-laterally on pronotum.

Microsculpture convex dorsally, and convex or subconvex on ventral surface.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 57a), and in lateral view quite wide and round (Fig. 58). Setae of paramere short (Fig. 56b).

Measurements and proportions.— Two samples studied, data for one presented in Table 45.

Variation.— Adults from Inuvik, Northwest Territories are most similar to those from eastern Siberia. Both samples show three color forms in similar proportion. I found no evidence of clinal variation in any characters.

All Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by paler parietale: dark brown only near frontale and epicranial suture.

First Instar Larvae

Description.— Parietale pale except near frontale and epicranial suture; nota and terga dark brown. Apical inner margin of mandible and posterior margin of retinaculum smooth; retinaculum normal (about twice as wide as long). Seta MP and EM-P of frontale very small. Epicranial suture 0.4 to 0.5 as long as antennomrere 1. Parietale with widespread microsculpture laterally (80% of dorsal and 30% of ventral surfaces), and with widespread pointed microsculpture laterally (50% of dorsal and 20% of ventral surfaces). Mesonotum and metanotum with pointed sculpture near suture. Sculpture of abdominal terga single-pointed.

Second Instar Larvae

Description.— Nota and terga dark brown. Parietale with widespread microsculpture laterally (30% of dorsal and 15% of ventral surfaces), and with restricted pointed microsculpture laterally (5% of dorsal and 15% of ventral surfaces). Each sclerite of pronotum with about 45 accessory setae, and with pointed microsculpture on lateral band. Mesonotum and metanotum with seta PIE-A small; each sclerite with about 40 accessory setae and lateral band with one to five accessory setae; pointed microsculpture widespread laterally (20% of surface) and moderately widespread near suture (10% of surface). Largest projection of urogomphus small in lateral view: 0.5 as long as width of urogomphus below. Each sclerite of terga 1 to 8 with about 30 accessory setae. Urogomphus with numerous very small accessory setae. Base of tergum 10 with coarse multi-pointed microsculpture. Abdominal epipleura 2 to 7 with 10 to 15 accessory setae; microsculpture multi-pointed. Abdominal hypopleura 2 to 7 with six to eight accessory setae, and largest ones small. Membrane microsculpture coarse.

Third Instar Larvae

Description.— Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with restricted pointed microsculpture latero-ventrally (5% of disc surface). Each sclerite of pronotum with about 60 accessory setae. Each sclerite of mesonotum and metanotum with more than 50 accessory setae, with widespread pointed microsculpture laterally (20 to 25% of surface) and without pointed microsculpture near suture. Lateral band of terga 1 to 8 narrow, not enlarged posteriorly, with about 12 accessory setae; terga 1 to 8 with about 45 accessory setae on each sclerite. Abdominal epipleuron 1 with 10 to 12 accessory setae, and epipleura 2 to 7 with about 25. Abdominal hypopleura 2 to 7 with about 20 accessory setae.

Geographical Distribution and Affinities, and Notes

Distribution.— This subarctic subspecies ranges from the Lena River in eastern Siberia to the Bering Sea, and from Alaska to the MacKenzie Delta, Northwest Territories. The North American distribution is illustrated in Fig. 173.

Taxonomic notes.— I have seen one seemingly original Sahlberg specimen. It matches adults of this subspecies. I have not seen the type of *E. angustatus,* but it came from a locality inside the range of this subspecies.

I have studied about 250 adults and dissected six males. I examined four first instar, four second instar and six third instar larvae from Inuvik, Northwest Territories.

Collecting notes.— Adults are less hygrophilous, are found on upper beaches, and run in sunny locations on bare soil with sparse *Equisetum fluviatile* Linnaeus, or on soil with some leaf litter in the willow zone. At Inuvik, Northwest Territories, adults were found only near the MacKenzie River on silty banks. Adults of this subspecies seem restricted to large subarctic rivers. Lindroth (1961) observed that wings are variable in length, and may not be functional.

Geographical affinities.— The range of this subspecies overlaps only that of *E. purpurans.*

Elaphrus angusticollis longicollis Sahlberg
Fig. 57a-b

Elaphrus longicollis J. Sahlberg, 1880:11. Type locality: Turuchansk on Yenisey River (western Siberia) subsequently designated by Lindroth (1961); lectotype, female from the same locality designated by Lindroth and deposited at the Swedish Ricksmuseum, Stockholm. Semenov, 1895:307. 1904c:104. Jacobson, 1906:268. Palmén, 1944:24. Lindroth, 1961:120.

Elaphrus jakovlewi Semenov, 1895:303. Type locality: Jamburg near Leningrad, USSR; type not seen. Semenov, 1897:596. 1904c:104. Lindroth, 1961:120.

Elaphrus jakovlewi ab. *costulatus* Semenov, 1895:305. Semenov does not suggest a type locality or type specimen.

Elaphrus jakowlewi; Lindroth, 1939:66. Palmén, 1944:24. Invalid emendation.

Adults

Diagnostic combination.— Distinguished from adults of *E. angusticollis angusticollis* as follows: elytral mirror flat; punctures sparse on elytral intervals 4, 6 and 8 (30 to 40 microns

Table 46. Descriptive statistics for *E. angusticollis longicollis*, based on ten males and ten females from USSR (Salmi, Suomi, Metsäpertti).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.42–1.67	1.56	0.106	0.032	4.5
PW	1.45–1.72	1.59	0.124	0.037	5.2
EL	3.50–4.25	3.84	0.288	0.085	3.9
EW	1.30–1.62	1.45	0.123	0.037	5.7
HW	1.72–2.02	1.86	0.115	0.034	4.1
B. Proportions					
PL/PW	0.913–1.031	0.979	0.045	0.014	3.1
PL/EL	0.375–0.434	0.407	0.018	0.006	2.9
PL/EW	1.017–1.143	1.078	0.049	0.014	3.1
PL/HW	0.800–0.877	0.836	0.036	0.010	2.9
PW/EL	0.375–0.433	0.416	0.019	0.006	3.1
PW/EW	1.017–1.140	1.101	0.043	0.012	2.6
PW/HW	0.811–0.901	0.854	0.033	0.010	2.6
EL/EW	2.571–2.731	2.648	0.070	0.022	1.8
EL/HW	1.973–2.162	2.054	0.072	0.022	2.3
EW/HW	0.732–0.803	0.776	0.031	0.010	2.7

apart); few accessory setae on hind coxa (two to five), lacking laterally on metasternum, and on abdominal sterna 4, 5 and 6 (one to eight).

Description.— One color form – dark blue-gray: microsculptured surfaces forming mosaic of dark copper, purple and black surfaces dorsally; punctures green or blue-green.

Abdominal sterna 4, 5 and 6 with one to eight accessory setae. Elytral mirrors in three rows and flat. Elytral pits not impressed and slightly outlined.

Integument sculpture. Punctures 15 to 20 microns in diameter dorsally. Punctures 30 to 40 microns apart on intervals 4, 6 and 8, 10 to 20 microns apart in pits, and 50 to 70 microns apart antero-laterally on pronotum.

Male genitalia. Apex angular, otherwise as that of *E. angusticollis angusticollis* (Fig. 57b).

Measurements and proportion.— One sample studied. See Table 46.

Variation.— Specimens from the Baltic sea and the Yenisey River are similar. There is no evidence of clinal variation in any characters.

Distribution.— A Palaearctic subspecies known in subarctic region from the Baltic Sea to Yenisey River.

Taxonomic notes.— I have seen adults of this subspecies from the type locality of *E. jakovlewi* and from Dudinka near type locality of *E. longicollis*. Therefore both names are probably synonymous.

I have examined about 40 adults and dissected five males.

Collecting notes.— Habitat similar to that of *E. angusticollis angusticollis*, but adults are found in the shade of taller vegetation (Palmén and Platonoff, 1943).

Geographical affinities.— The range does not overlap that of other species.

Table 47. Descriptive statistics for *E. ulrichi*, based on ten males and ten females from Carinthia, Austria.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.35–1.90	1.73	0.166	0.050	6.4
PW	1.37–1.90	1.78	0.180	0.054	6.7
EL	4.05–4.85	4.44	0.257	0.077	3.8
EW	1.42–1.67	1.58	0.096	0.029	4.0
HW	1.70–2.22	2.08	0.169	0.050	5.4
B. Proportions					
PL/PW	0.932–1.015	0.970	0.033	0.010	2.3
PL/EL	0.293–0.422	0.390	0.039	0.012	6.7
PL/EW	0.806–1.169	1.094	0.112	0.034	6.8
PL/HW	0.614–1.059	0.833	0.113	0.034	9.1
PW/EL	0.299–0.432	0.402	0.040	0.012	6.7
PW/EW	0.821–1.206	1.127	0.118	0.036	7.0
PW/HW	0.625–1.088	0.858	0.117	0.036	9.1
EL/EW	2.656–3.018	2.803	0.124	0.038	3.0
EL/HW	1.952–2.676	2.134	0.208	0.062	6.5
EW/HW	0.695–0.971	0.762	0.079	0.034	6.9

Elaphrus ulrichi Redtenbacher

Figs. 59a-b, 103a-b

Elaphrus ulrichi Redtenbacher, 1842:5. Type area: Austria: type not seen. Letzner, 1849:52. Schaum, 1856:73. Redtenbacher, 1874:6. Seidlitz, 1875:2. Dalla-Torre, 1877:23. Fauvel, 1882:82, 83. Marseul, 1882:4. Reitter, 1887:17. Seidlitz, 1891:20. Ganglbauer, 1892:123, 124. Semenov, 1895:306, 317. Jacobson, 1096:268. Reitter, 1908:96, 97. 1909:106. Kuhnt, 1912:50. Schaufuss, 1916:29. Porta, 1923:78.

Elaphrus ulrichii Gaubil, 1849:14 (invalid emendation).

Elaphrus smaragdinus Knorlein (*In*: Schaum, 1856:73). NOMEN NUDUM.

Elaphrus austriacus Ulrick (*In*: Schaum, 1856:73). NOMEN NUDUM. Semenov, 1895:317.

Elaphrus beraneki Reitter, 1887:242. Type area: Czechoslovakia in Tabor, Bohemia; type not seen. Ganglbauer, 1892:123, 124. Jacobson, 1906:268.

Elaphrus baraneki Semenov, 1895:317 (invalid emendation).

Elaphrus ullrichi Semenov, 1895:317 (invalid emendation).

Adults

Diagnostic combination.— Distinguished from adults of other species by lack of setigerous puncture near hind angle of pronotum, and by lack of accessory setae along posterior area of metasternum.

Description.— Dorsal surface emerald green with numerous copper reflecting surfaces. Microsculptured areas copper (darker on elytral intervals and brighter on pronotum) and green. Punctures green or blue-green, but purple in elytral pits. Elytra appearing brighter green laterally resulting from nearly black microsculptured surfaces with green punctures. Elytral pits sharply outlined against dark copper intervals. Femora red-brown with dorsal side bright green.

Antennomere 4 with few apical setae mostly on posterior side. Pronotum with lateral margin unbeaded but traceable, without setigerous puncture on hind angle, and without medial impression. Prosternal process without accessory setae. Metasternum with few accessory setae antero-medially, and without setae posteriorly. Abdominal sterna 4, 5 and 6 with

less than 4 accessory setae. Elytral mirrors in one or two rows, clearly outlined and flat; first, or first and third sutural mirrors wider. Elytral pits slightly impressed and sharply outlined against darker intervals. Secondary sexual characters in males typical of genus. Trochanter of midleg with one seta. Tibia of foreleg without projection at base of posterior spur.

Integument sculpture. Punctures 15 to 20 microns in diameter on elytra and head, 25 to 30 microns in diameter on pronotum and ventral surfaces. Punctures 5 to 10 microns apart on elytra, and 10 to 20 microns apart medially and 50 to 100 microns apart laterally on pronotum.

Microsculpture subconvex on green, blue-green and purple surfaces and flat on or absent from copper and ventral surfaces.

Male genitalia. Apex of median lobe in ventral view thin-edged and slightly twisted (Fig. 59a) and in lateral view very wide with ventral bulge (Fig. 59b). Setae of parameres long (Fig. 56b).

Measurements and proportions.— I studied one sample, see Table 47.

Variation.— I observed no evidence of geographical variation.

First Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by red-brown anterior portion of pronotum and tergum 1 (Bauer 1976), and by multipointed microsculpture on abdominal terga.

Description.— Anterior portion of pronotum and tergum 1 red-brown; except for pale areas at base of parietale and behind eyes, head, nota and terga dark brown (Bauer, 1976). Apical inner margin of mandible and posterior margin of retinaculum smooth; retinaculum normal (about twice as wide as long). Seta MP and EM-P on frontale very small. Epicranial suture 0.4 to 0.5 length of antennomere 1. Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with widespread pointed microsculpture laterally (20% of dorsal and 10% of ventral surfaces). Mesonotum and metanotum without pointed sculpture. Microculpture on abdominal terga multipointed.

Second and Third Instar Larvae

Diagnostic combination.— Distinguished from larvae of other species by unusual dorsal coloration: pronotum, tergum 1 and lateral 0.3 of terga 2 to 7 reddish-brown, rest dark brown.

Second Instar Larvae

Description.— Pronotum, tergum 1 and external 0 .3 of terga 2 to 7 red-brown, mesonotum, metanotum, inner 0.7 of terga 2 to 7, and tergum 9 dark brown.

Parietale with widespread microsculpture laterally (50% of dorsal and 20% of ventral surfaces), and with moderately widespread pointed microsculpture (5% of dorsal and 15% of ventral surfaces). Each sclerite of pronotum with about 45 accessory setae, and with pointed microsculpture on lateral band. Mesonotum and metanotum with setae PIE-A small; each sclerite with about 40 accessory setae, and lateral band with one to five accessory setae; pointed sculpture widespread laterally (20% of surface), moderately widespread near suture(10% of surface). Largest projection of urogomphus in lateral view absent or barely apparent (Fig. 103a). Each sclerite of terga 1 to 8 with about 30 accessory setae. Urogomphus with numerous very small accessory setae. Base of tergum 10 with scale-like and meshed microsculpture. Abdominal epipleura 2 to 7 with more than 15 accessory setae; microsculpture multi-pointed. Abdominal hypopleura 2 to 7 with eight or more small accessory setae. Membrane with barely suggested pointed microsculpture at high magnification (250 X).

Third Instar Larvae

Description.— Parietale with widespread microsculpture laterally (60% of dorsal and 15% of ventral surfaces), and without pointed microsculpture. Each sclerite of pronotum with about 60 accessory setae. Mesonotum and metanotum with pointed microsculpture restricted laterally (5% of surface), and absent near suture. Terga 1 to 8 with lateral band enlarged (wider posteriorly), and with more than 15 accessory setae. Abdominal epipleuron 1 with four accessory setae, and epipleura 2 to 7 each with about 40. Abdominal hypopleura 2 to 7 each with about 20 accessory setae.

Geographical Distribution and Affinties, and Notes

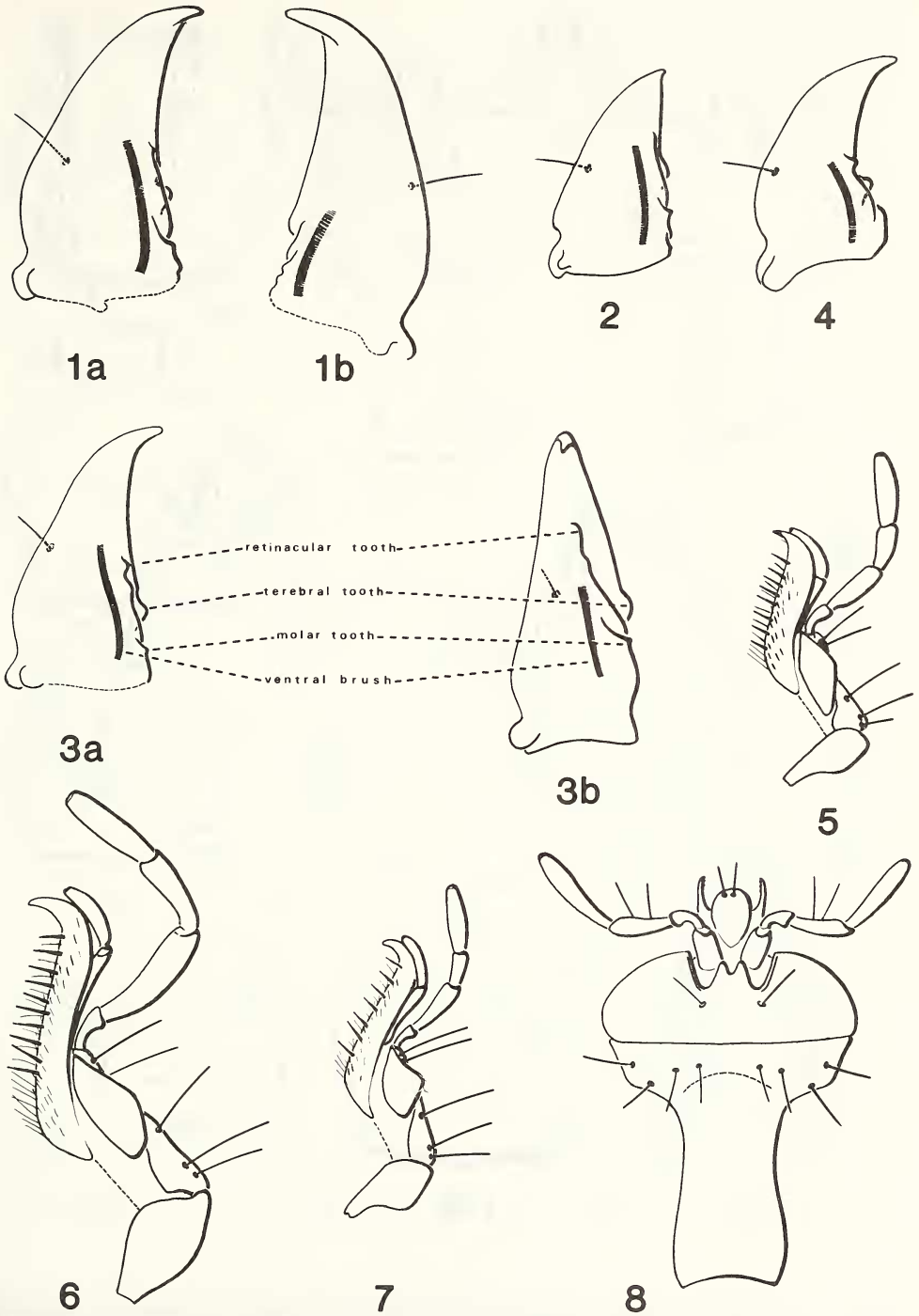
Distribution.— A middle European species recorded from The Netherlands, eastern France, northern Italy, Switzerland, Austria, Germany, Poland, Hungary and Czechoslovakia (Turin, *et al.*, 1977). I have not seen specimens from Italy, Poland, Hungary and The Netherlands.

Taxonomic notes.— *E. ulrichi* is easily distinguished from the original description. According to the description of *E. beraneki,* the type is apparently a dark color variant.

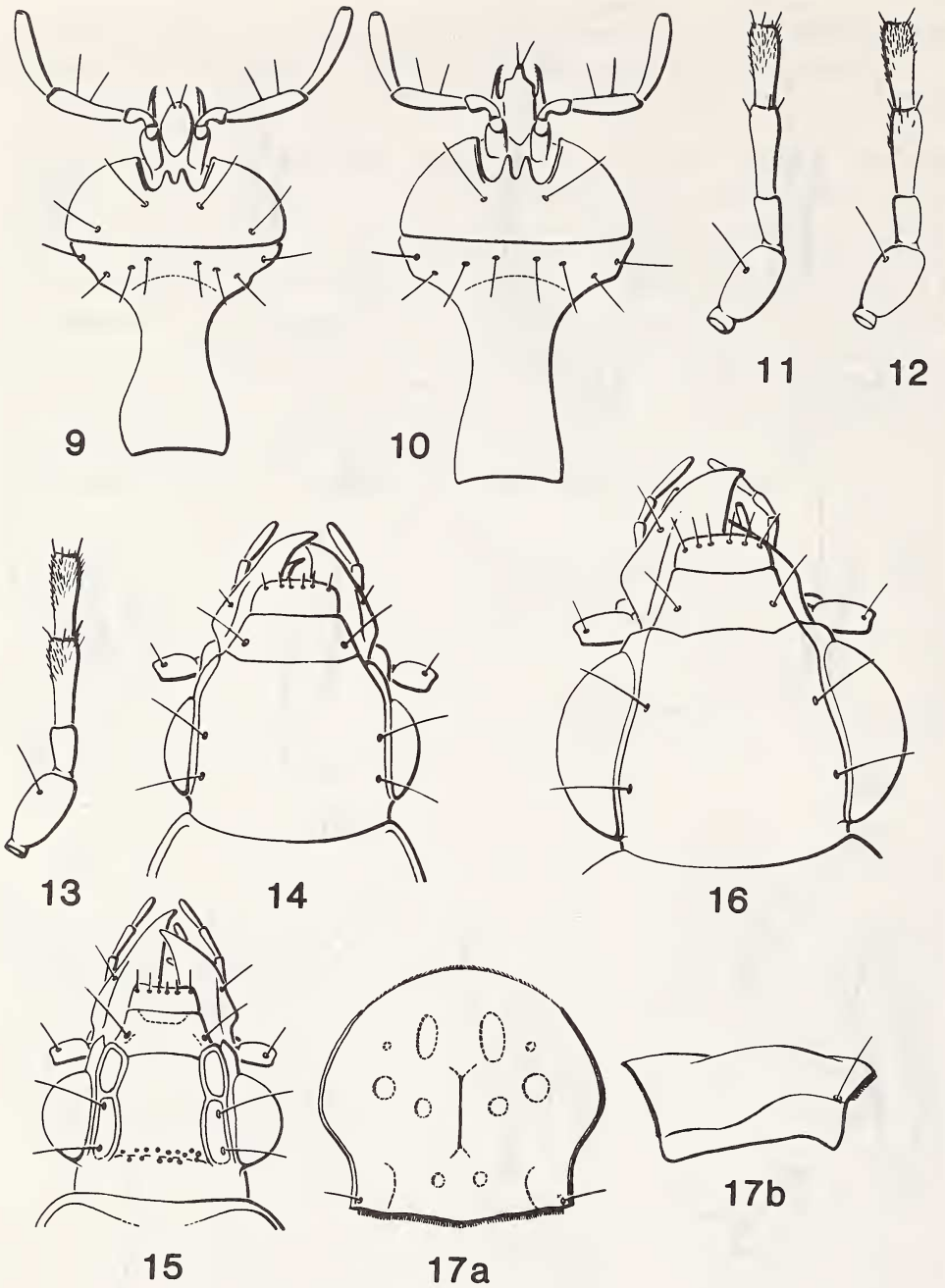
I studied about 60 adults and dissected three males. I examined three first instar, one second and one third instar larvae from Austria.

Collecting notes.— Adults of this species are found away from water on firm sandy overflows with scattered vegetation along mountain rivers with moderate current (Bauer, 1976). Bauer (1976) observed that larvae, especially of the second and third instar, match the color pattern of adults of poisonous staphylinids *Paederus ruficollis* Fabricius. Smetana (1949) collected adults of *E. ulrichi* in a similar habitat in Czechoslovakia, along with adults of *P. ruficollis* and those of a larger species *P. rubrothoracicus* Goeze. Adults of *P. ruficollis* are similar in size to second instar larvae of *E. ulrichi,* and of *P. rubrothoracicus* and to third instar larvae of *E. ulrichi.* Bauer (1976) showed that *P. ruficollis* is strongly avoided by *Actitis hypoleucos* (Linneaus), a common species of bird in this habitat. Thus, he suggested that the larval colors are possibly the result of mimicry.

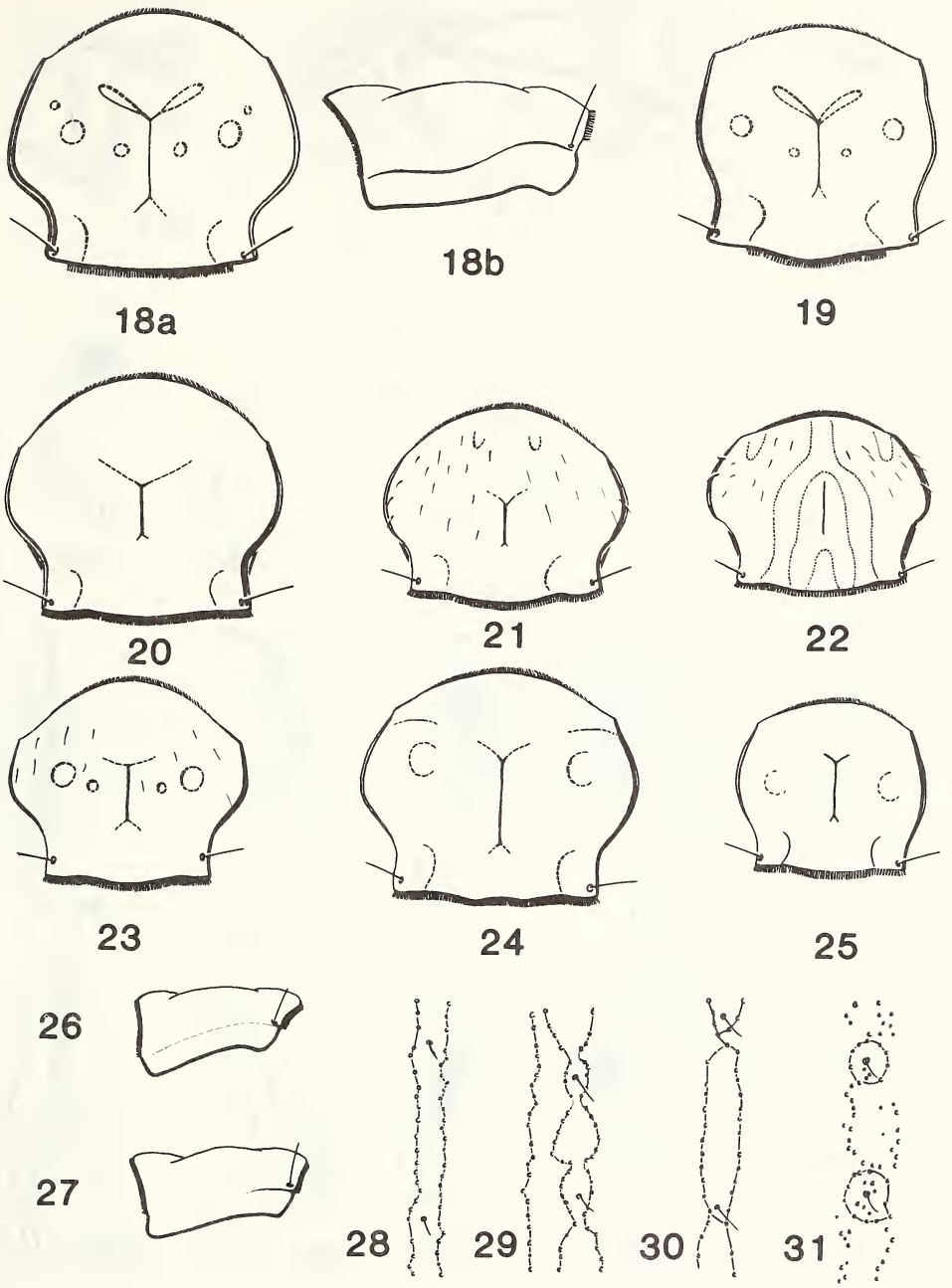
Geographical affinities.— The ranges of this species and *E. aureus* overlap.



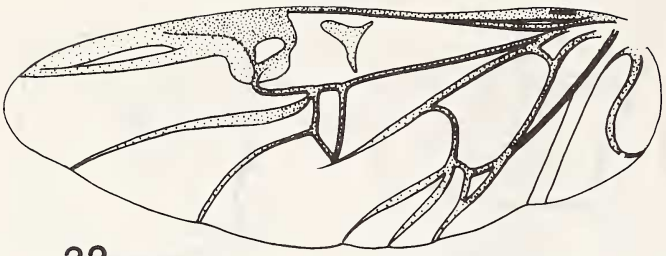
Figs. 1–8. Line drawings of mouthparts of adult Elaphrini. Figs. 1–4. Mandibles. 1. Mandible of *B. quadricolis* Haldeman, ventral aspect, a) right, b) left. 2. Right mandible of *D. polita* Faldermann, ventral aspect. 3. Right mandible of *E. lapponicus* Gyllenhal, a) ventral aspect, b) inner aspect. 4. Right mandible of *E. parviceps* Van Dyke, ventral aspect. Figs. 5–7. Maxillae, ventral aspect. 5. *D. polita* Faldermann. 6. *B. quadricollis* Haldeman. 7. *E. lapponicus* Gyllenhal. Fig. 8. Gula and labium of *D. polita* Faldermann, ventral aspect.



Figs. 9–17. Line drawings of structures of adult Elaphrini. Figs. 9–10. Gula and labium, ventral aspect. 9. *B. quadricollis* Haldeman. 10. *E. lapponicus* Gyllenahl. Figs. 11–13. Antennomeres 1-4, dorsal aspect. 11. *E. riparius* Linnaeus 12. *E. parviceps* Van Dyke. 13. *E. lecontei* Crotch. Figs. 14–16. Head, dorsal aspect. 14. *D. polita* Faldermann. 15. *B. multipunctata* Linnaeus. 16. *E. lapponicus* Gyllenhal. Fig. 17. Pronotum of *E. uliginosus* Fabricius, a) dorsal aspect, b) lateral aspect.



Figs. 18–31. Line drawings of pronota and elytra of adult Elaphrini. Fig. 18. Pronotum of *E. fuliginosus* Say, a)dorsal aspect, b) lateral aspect. Figs. 19–25. Pronotum, dorsal aspect. 19. *E. cupreus* Duftschmid. 20. *E. marginicollis* n. sp. 21. *E. mimus* n. sp. 22. *E. viridis* Horn. 23. *E. lheritieri* Antoine. 24 *E. lecontei* Crotch. 25. *E. riparius* Linnaeus. Figs. 26–27. Pronotum, lateral aspect. 26. *E. angusticollis angusticollis* Sahlberg 27. *E. purpurans* Hausen. Figs. 28–31. Elytral striae 2 (right) and 3 (left), discal portion. 28. *D. polita* Faldermann. 29. *B. eschscholtzi* Zoubkoff. 30. *B. quadricollis* Haldeman. 31. *E. lapponicus* Gyllenhal.



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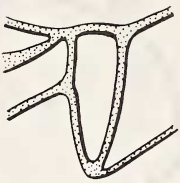

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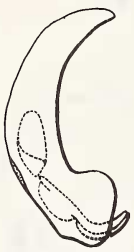

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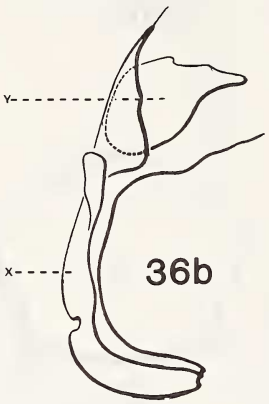

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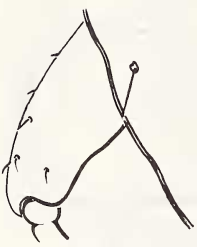

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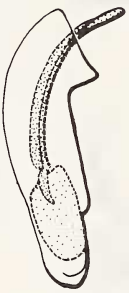

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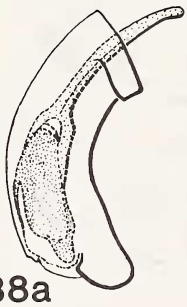

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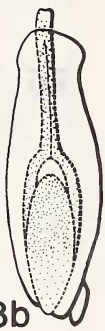
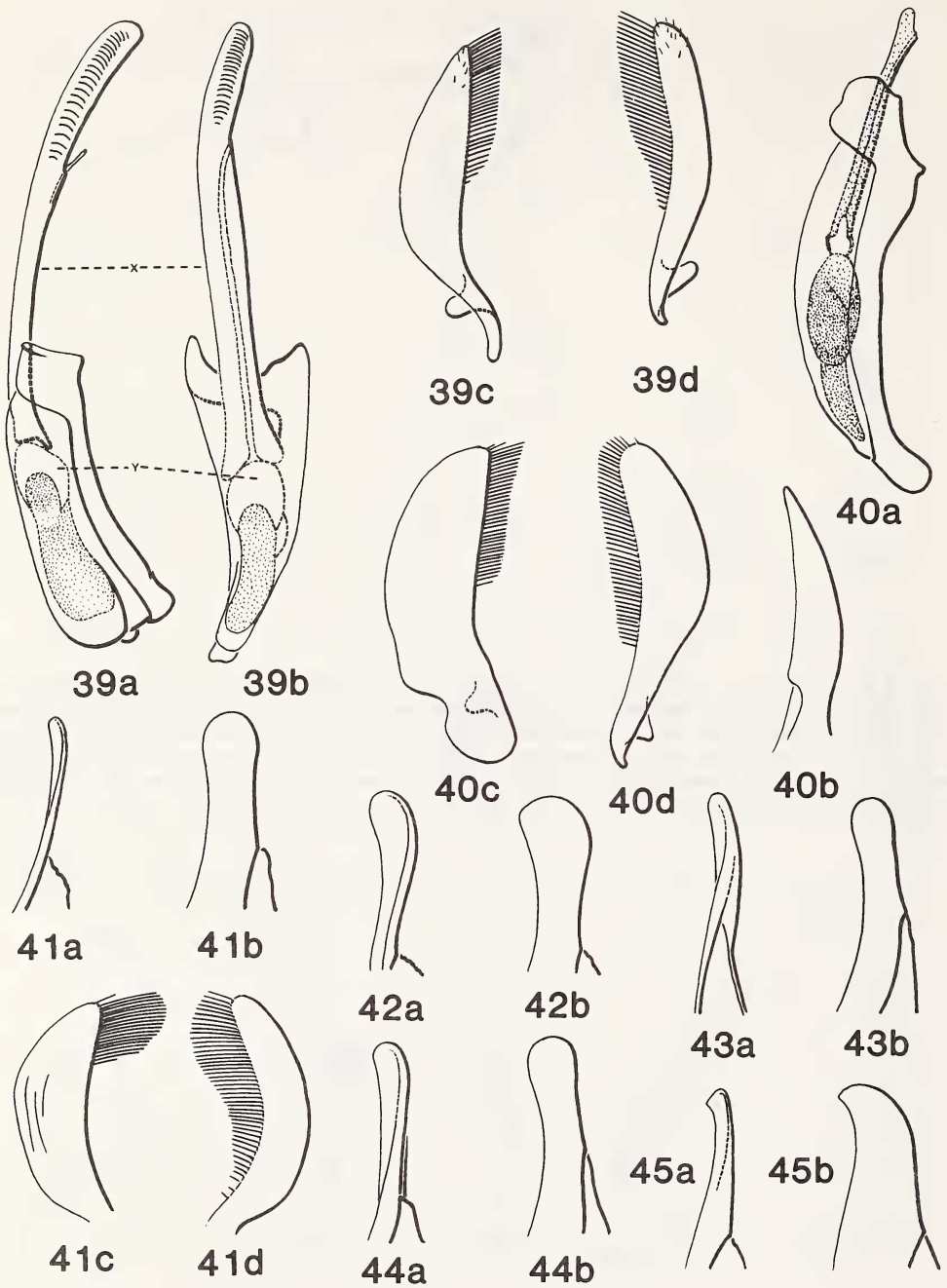
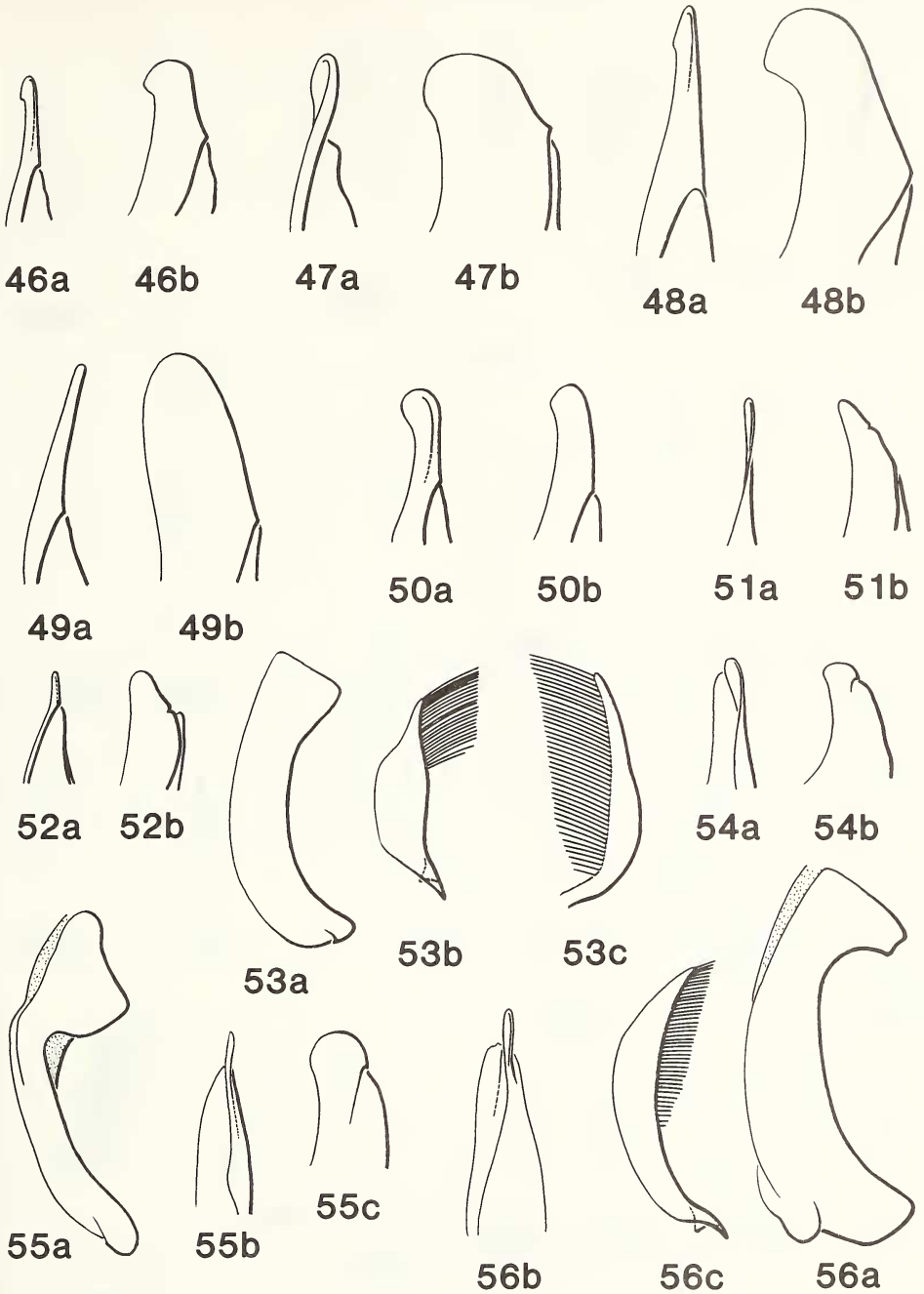


38b

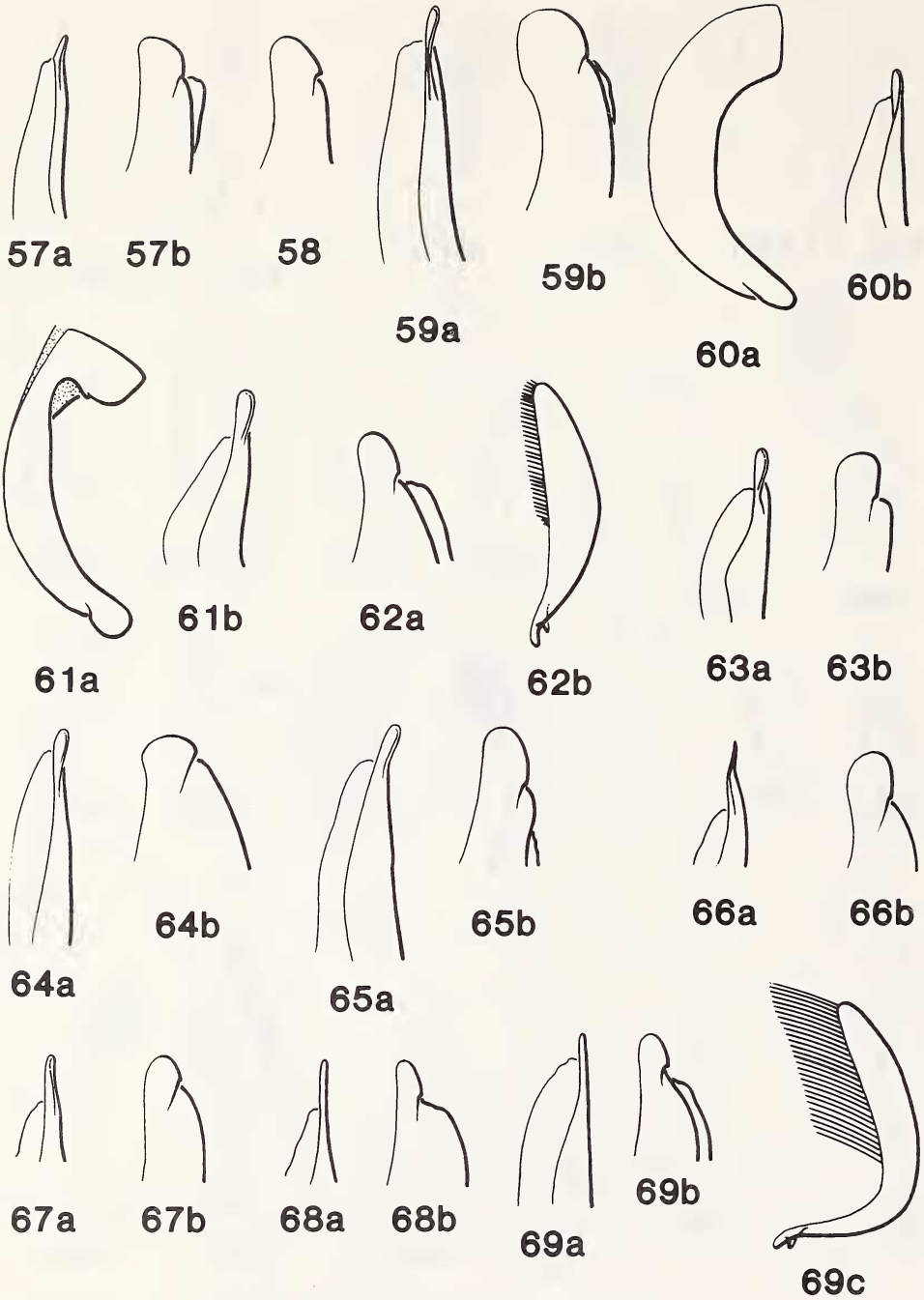
Figs. 32–38. Line drawings of structures of adult Elaphrini. Figs. 32–33. Hindwing. 32. *E. americanus* Dejean. 33. Oblongum of *B. multipunctata* Linnaeus. Figs. 34–35. Dorso-subapical surface of hind femur. 34. *E. americanus* Dejean. 35. *E. californicus* Mannerheim. Fig. 36. Male genitalia of *Broscus cephalotes* (redrawn from Ball, 1956), a) median lobe lateral aspect, b) detail of internal sac (inverted) showing sclerites X and Y, lateral view, c) left paramere, d) right paramere. Figs. 37–38. Male genitalia, a) lateral aspect of median lobe and internal sac, b) dorsal aspect of median lobe and internal sac c) left paramere, d) right paramere. 37. Melaenus piger. 38. *D. arctica* Gyllenhal.



Figs. 39–45. Line drawings of male genitalia of adult Elaphrini. Figs. 39–40. Median lobe and internal sac, a) lateral aspect, b) dorsal aspect; c) left paramere, d) right paramere. 39. *B. multipunctata* Linnaeus. 40. *E. lapponicus obliteratus* Mannerheim. Fig. 41. *E. splendidus* Fischer von Waldheim. a) apex of median lobe, dorsal aspect, b) apex of median lobe, lateral aspect, c) left paramere, d) right paramere. Figs. 42–45. Apex of median lobe, a) dorsal aspect, b) lateral aspect. 42. *E. japonicus* Uéno. 43. *E. uliginosus* Fabricius. 44. *E. pyrenoeus* Motschulsky. 45. *E. fuliginosus* Say.



Figs. 46–56. Line drawings of male genitalia of adult Elaphrini. Figs. 46–52. Apex of median lobe, a) dorsal aspect, b) lateral aspect. 46. *E. lindrothi* n. sp. 47. *E. cicatricosus* LeConte. 48. *E. sibiricus* Motschulsky. 49. *E. cupreus* Duftschmid. 50. *E. clairvillei* Kirby. 51. *E. olivaceus* LeConte. 52. *E. laevigatus* LeConte. Fig. 53. *E. punctatus* Motschulsky, Japan, a) lateral aspect of median lobe, b) left paramere, c) right paramere. Fig. 54. Apex of median lobe of *E. punctatus* Motschulsky, Irkutsk, USSR, a) ventral aspect, b) lateral aspect. Fig. 55. Median lobe of *E. aureus* Müller, a) lateral aspect, b) ventral aspect of apex, c) lateral aspect of apex. Fig. 56. *E. purpurans* Hausen. a) lateral aspect of median lobe, b) ventral aspect of apex of median lobe, c) right paramere.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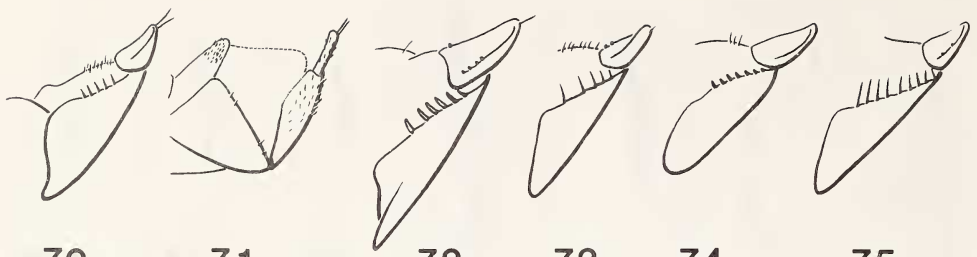
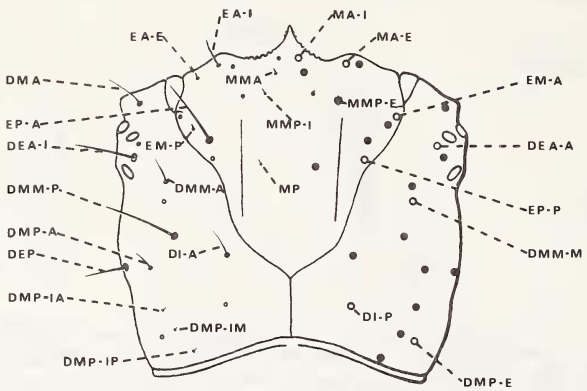
Figs. 57–69. Line drawings of male genitalia of adult Elaphrini. Fig. 57. Apex of median lobe of *E. angusticollis longicollis* Sahlberg, a) ventral aspect, b) lateral aspect. Fig. 58. Apex of median lobe of *E. angusticollis angusticollis* Sahlberg, . lateral aspect. Fig. 59. Apex of median lobe of *E. ulrichi* Redtenbacher, a) ventral aspect, b) lateral aspect. Figs. 60–61. Median lobe, a) lateral aspect, b) ventral aspect of apex. 60. *E. ruscarius* Say. 61. *E. riparius* Linnaeus. Fig. 62. *E. hypocrita* Semenov, a) lateral aspect of apex of median lobe, b) right paramere. Figs. 63–68. Apex of median lobe, a) ventral aspect, b) lateral aspect. 63. *E. comatus* n. sp., Harbin, China. 64. *E. lheritieri* Antoine. 65. *E. lecontei* Crotch. 66. *E. finitimus* Casey, Tocaloma, California. 67. *E. americanus* Dejean, Pullman, Washington. 68. *E. americanus* Dejean, Seattle, Washington. Fig. 69. *E. americanus* Dejean, Spring Creek Basin, Alberta, a) ventral aspect of median lobe, b) lateral aspect of median lobe, c) right paramere.





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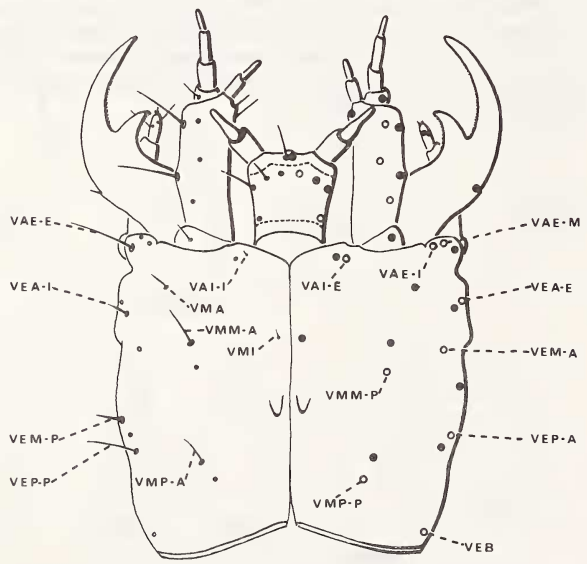

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Figs. 70–75. Line drawings of ovipositor styli, lateral aspect, of adult Elaphrini. 70. *D. polita* Faldermann. 71. *B. multipunctata* Linnaeus. 72. *E. lapponicus obliteratus* Mannerheim. 73. *E. clairvillei* Kirby. 74. *E. purpurans* Hausen. 75. *E. lecontei* Crotch. Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, a) dorsal aspect of the head, b) ventral aspect of the head. Setae and pores represented by black and pen circles respectively on the right side of figure.

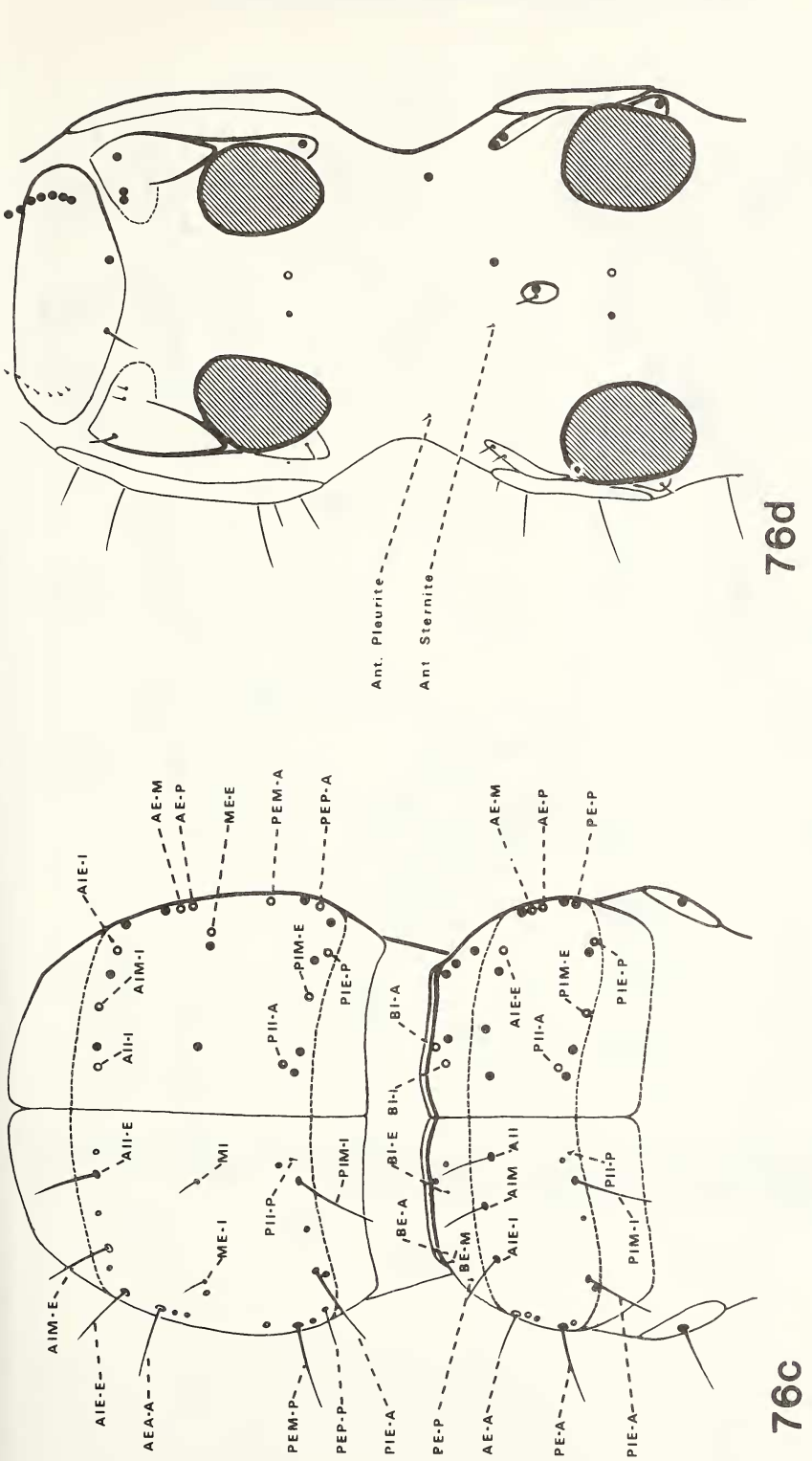


Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, c) dorsal aspect of prothorax and mesothorax, d) ventral aspect of prothorax and mesothorax. Setae and pores symbolized respectively by black and open circles on the right side of figure. Pale portions of nota and terga are termed "bands". The anterior band is anterior of the subapical dashed line in Fig. 76c; the posterior band is posterior to the sub-basal dashed line in Fig. 76c; the lateral band is the lateral portion as in Fig. 76d.

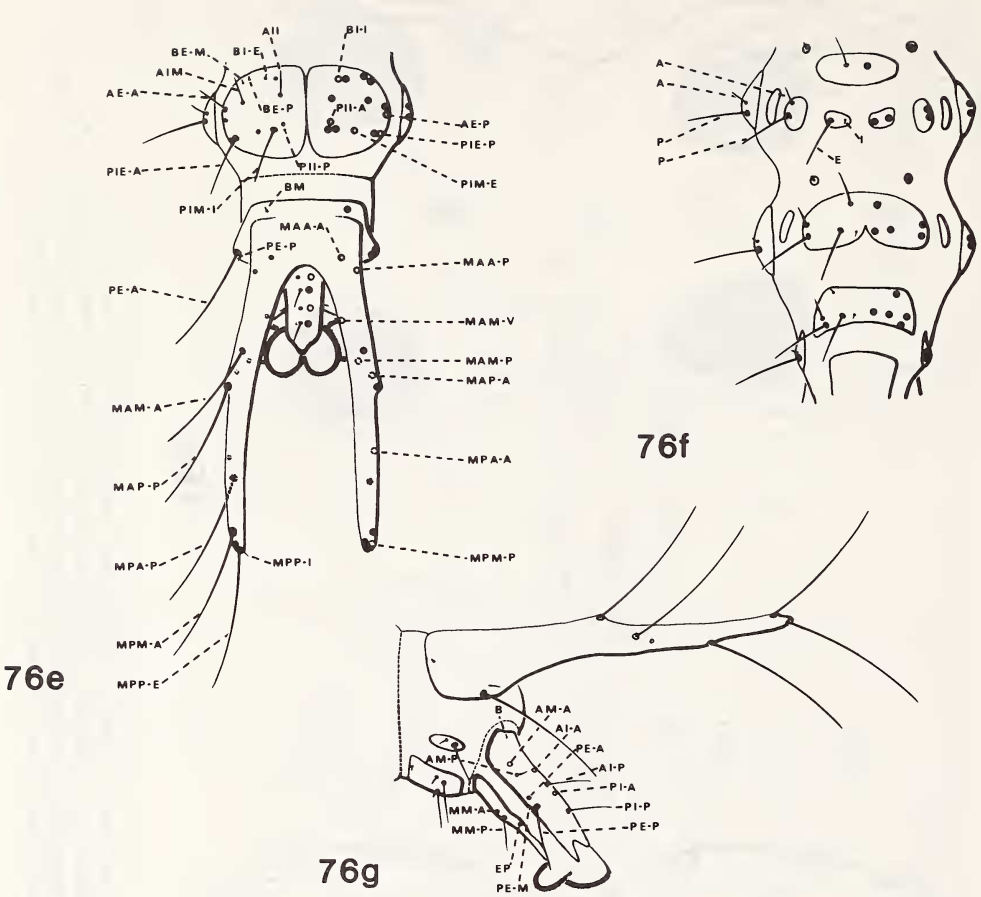
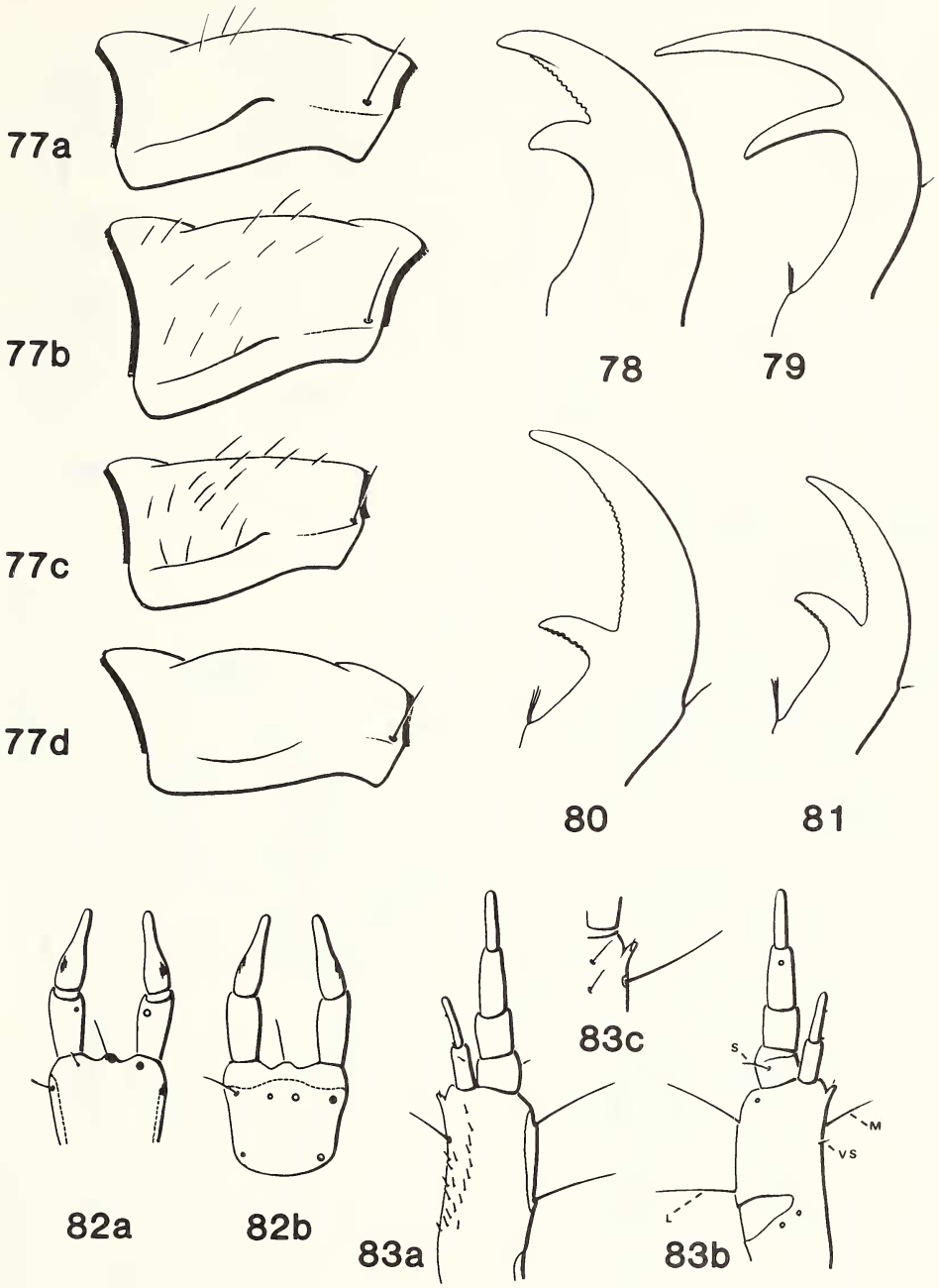


Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, e) dorsal aspect of abdominal segments 8, 9 and 10, f) ventral aspect of abdominal segments 7, 8 and 9, g) lateral aspect of abdominal segments 9 and 10. Setae and pores symbolized respectively by black and open circles on the right side of figure.



Figs. 77–83. Line drawings of structures of Elaphrini. Fig. 77. Lateral aspect of pronotum of adult a) *E. lheritieri* Antoine, b) *E. mimus* n. sp., c) *E. viridis* Horn, d) *E. californicus* Mannerheim. Figs. 78–81 Mandibles. 78. Third instar larva of *D. arctica* Gyllenhal (redrawn from Lindroth, 1954). 79. First instar larva of *D. polita* Faldermann. 80. First instar larva of *E. clairvillei* Kirby. 81. First instar larva of *E. lecontei* Crotch. Fig. 82. Labium of first instar larva of *E. clairvillei* Kirby, a) dorsal aspect, b) ventral aspect. Fig. 83. Maxilla of first instar larva of *D. polita* Faldermann, a) dorsal aspect, b) ventral aspect, c) lacinia. L= large seta, M= medium-sized seta, S= small seta, VS=very small seta.

84

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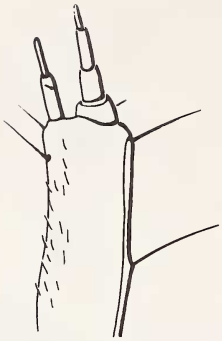

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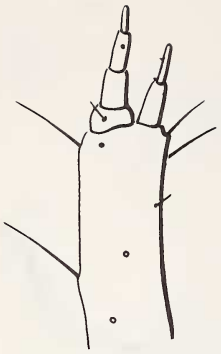

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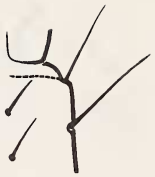

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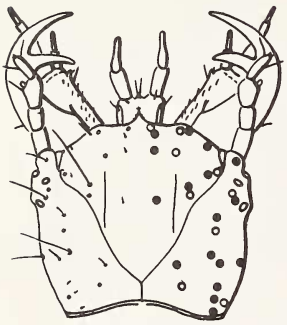

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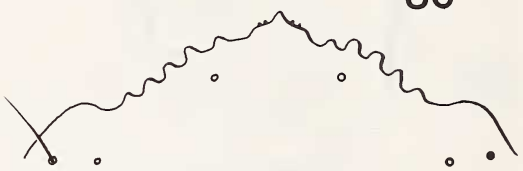

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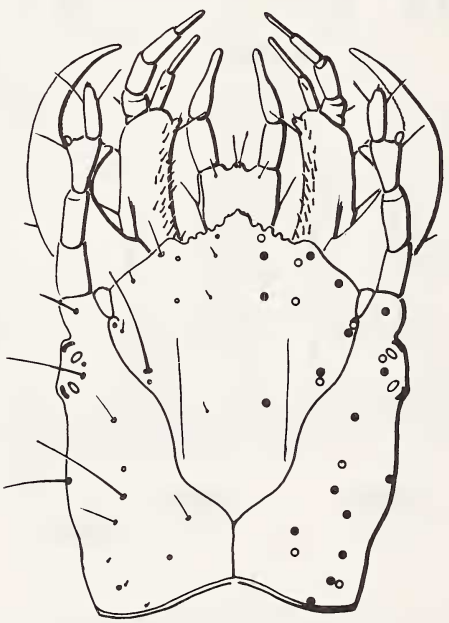
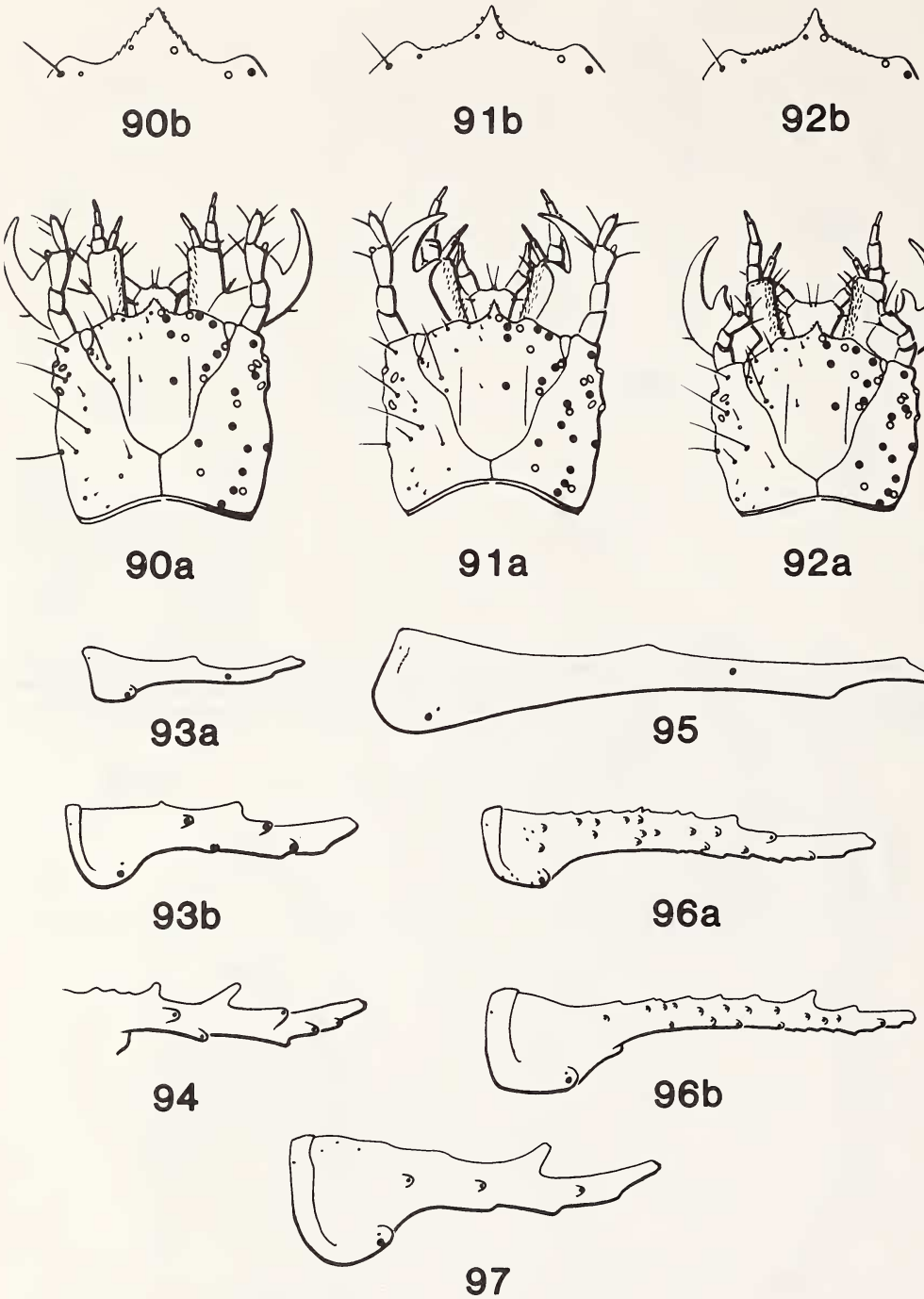
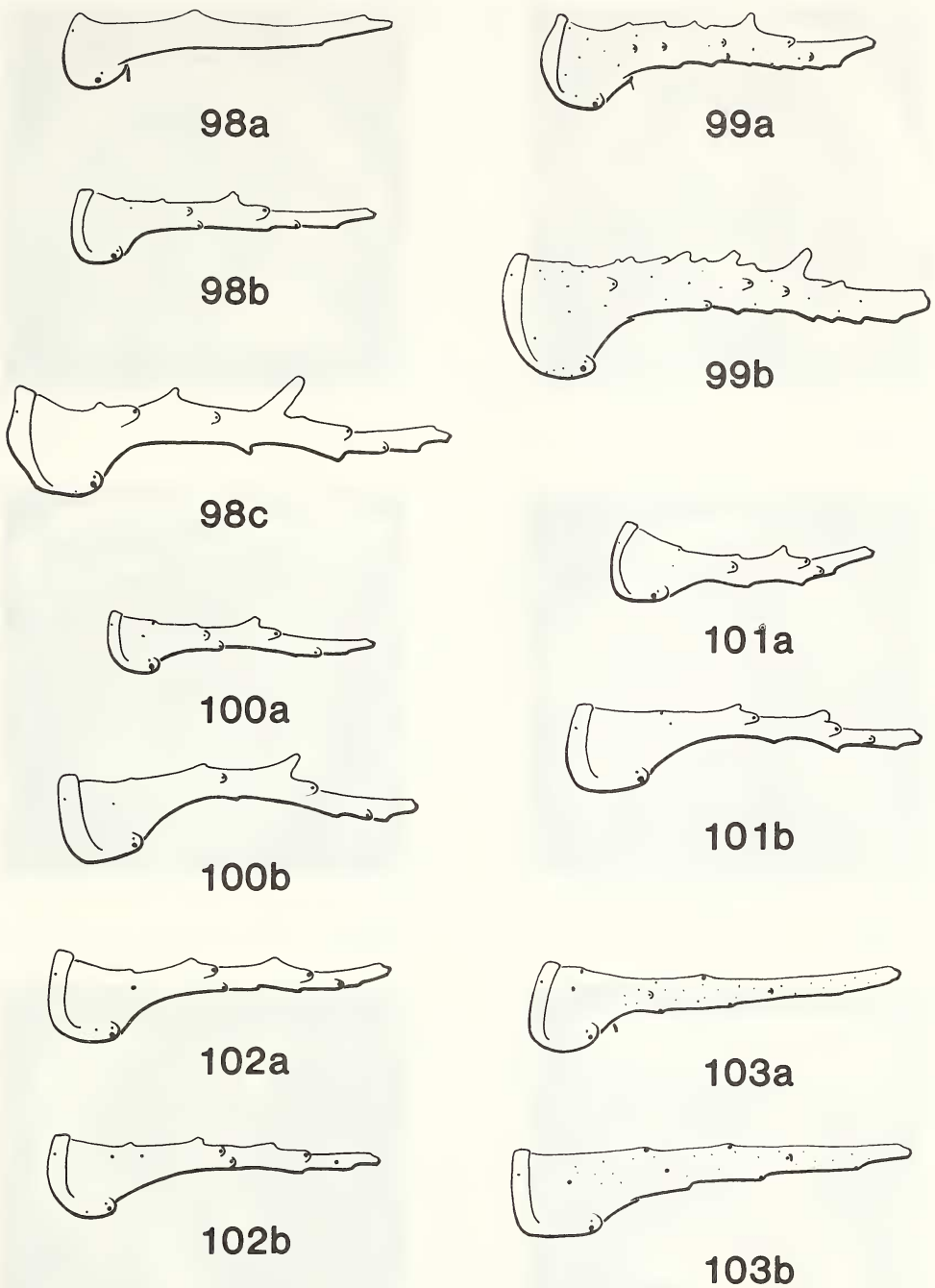


88a

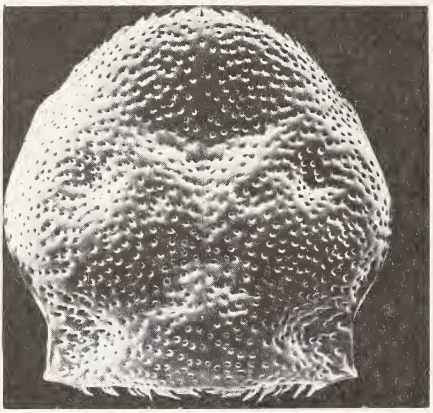
Figs. 84–89. Line drawings of head and mouthparts of larval Elaphrini. Fig. 84. Lacinia of *D. arctica* Gyllenhal (redrawn from Lindroth, 1954). Fig. 85. Maxilla of *E. clairvillei* Kirby, a) dorsal aspect, b) ventral aspect, c) lacinia. Fig. 86. Lacinia of *E. purpurans* Hausen. Figs. 87–89. Head, a) dorsal aspect, b) nasale. 87. *D. polita* Faldermann. 88. *B. quadricollis* Haldeman. 89. *E. lapponicus lapponicus* Gyllenhal.



Figs. 90–97. Line drawings of structures of larval Elaphrini. Figs. 90–92. Head, a) dorsal aspect, b) nasale. 90. *E. clairvillei* Kirby. 91. *E. lecontei* Crotch. 92. *E. purpurans* Hausen. Figs. 93–97. Abdominal tergum 9, lateral aspect. 93. *D. polita* Faldermann, a) first, b) second instar larva. 94. *D. arctica* Gyllenhal, third instar larva. 95. *B. quadricollis* Haldeman, first instar larva. 96. *B. multipunctata* Linnaeus, a) second, b) third instar larva. 97. *E. lapponicus lapponicus* Gyllenhal, third instar larva.



Figs. 98–103. Line drawings of abdominal tergum 9, lateral aspect, of larval Elaphrini. 98. *E. clairvillei* Kirby, a) first, b) second, c) third instar larva. 99. *E. cicatricosus* LeConte, a) second, b) third instar larva. 100. *E. americanus* Dejean, a) second, b) third instar larva. 101. *E. aureus* Müller, a) second, b) third instar larva. 102. *E. purpurans* Hausen, third instar larva, a) McMinnville, Oregon, b) Conjuring Creek, Alberta. 103. *E. ulrichi* Redtenbacher, a) second, b) third instar larva.



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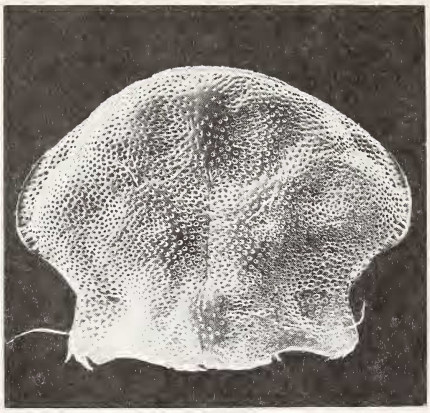

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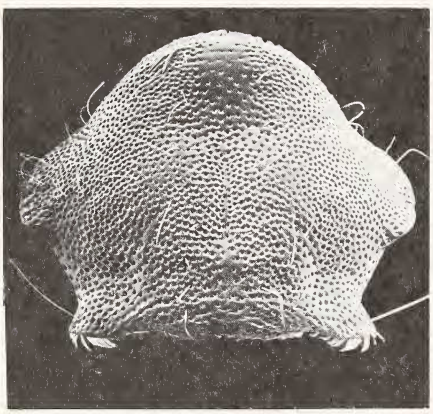

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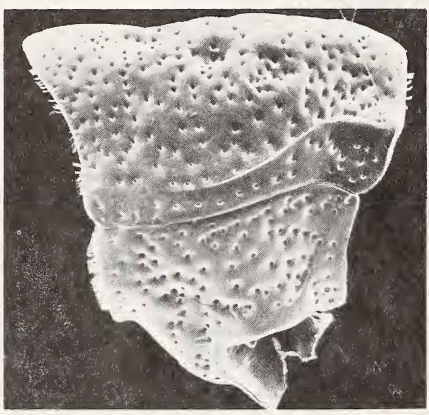

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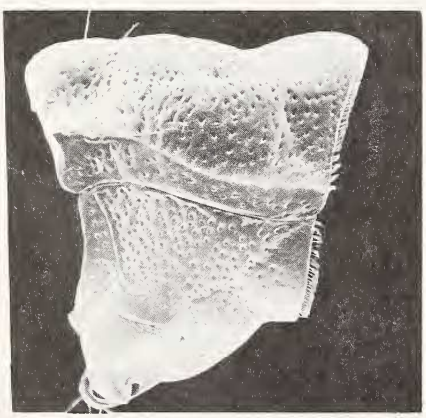

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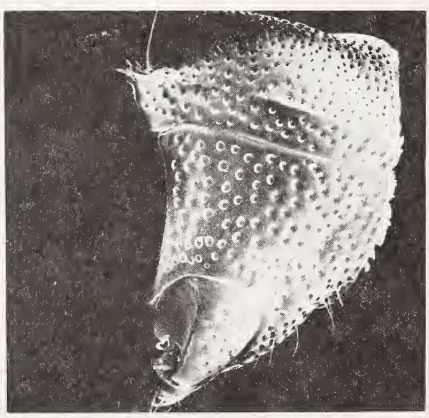

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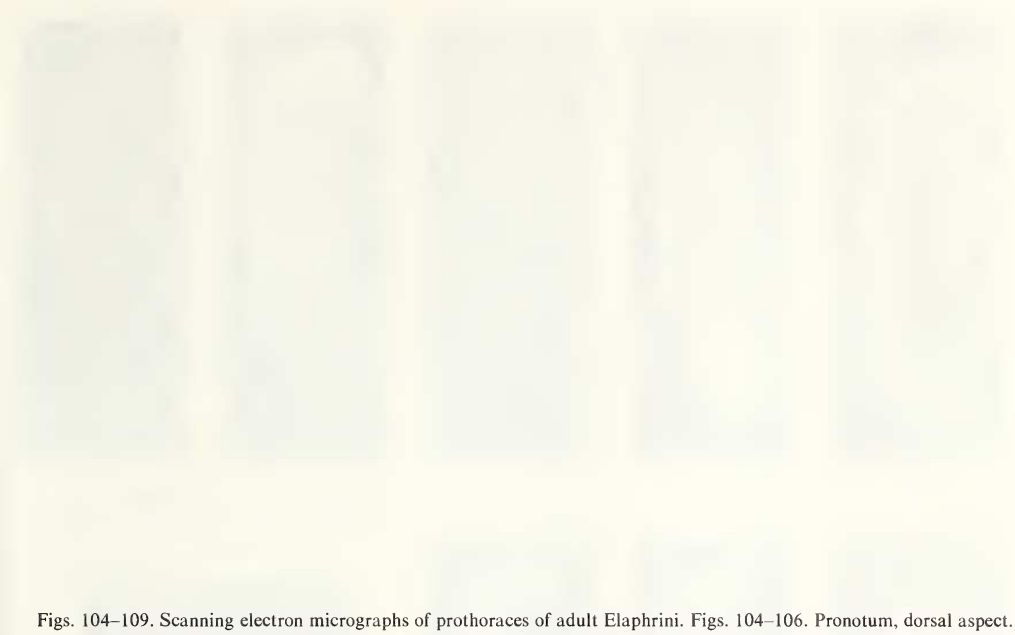

Figs. 104–109. Scanning electron micrographs of prothoraces of adult Elaphrini. Figs. 104–106. Pronotum, dorsal aspect. 104. *E. lindrothi* n. sp. 105. *E. lheritieri* Antoine. 106. *E. viridis* Horn. Figs. 107–109. Pronotum and prosternum, lateral aspect. 107. *E. cicatricosus* LeConte. 108. *E. cupreus* Duftschmid. 109. *E. ruscarius* Say.

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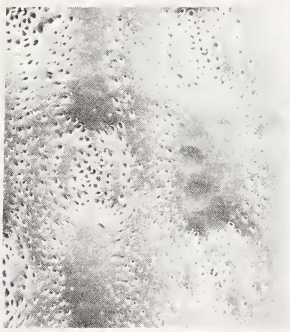

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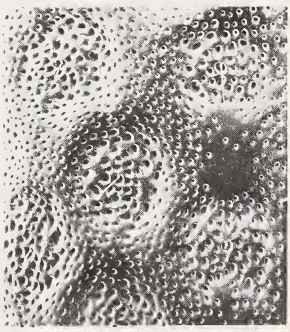

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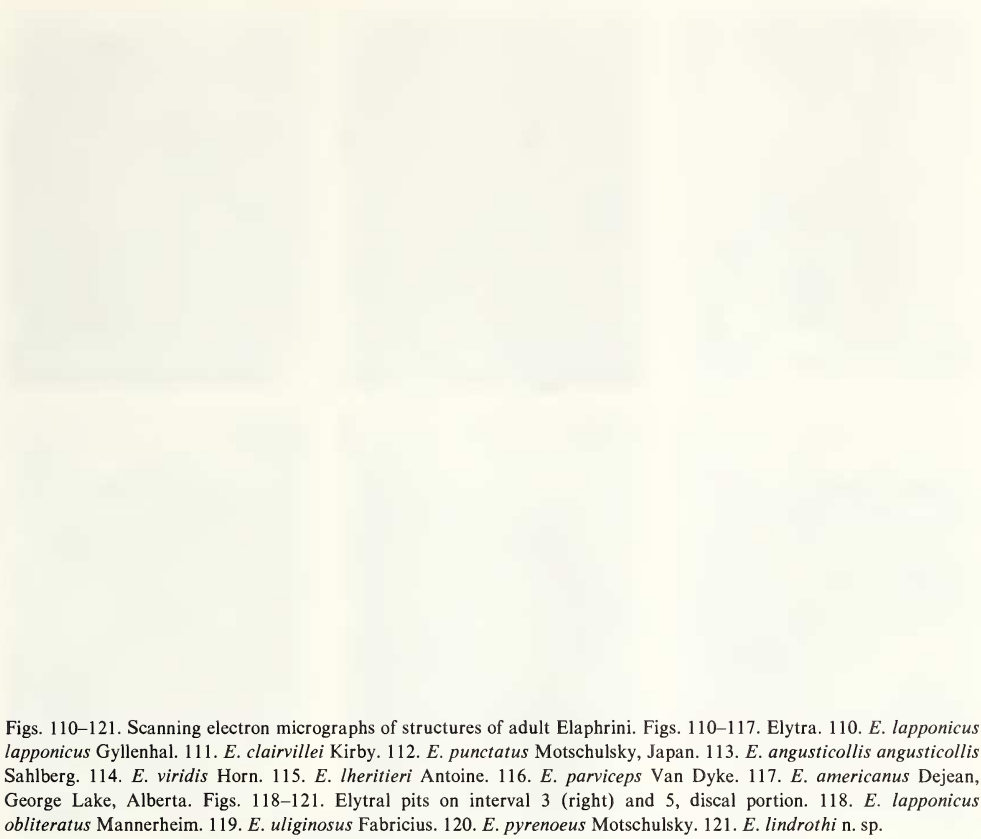
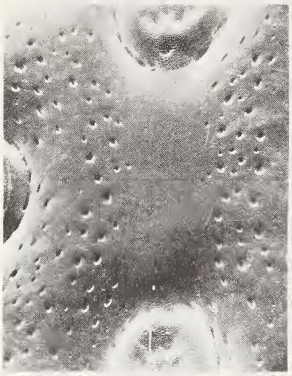


Figs. 110–121. Scanning electron micrographs of structures of adult Elaphrini. Figs. 110–117. Elytra. 110. *E. lapponicus lapponicus* Gyllenhal. 111. *E. clairvillei* Kirby. 112. *E. punctatus* Motschulsky, Japan. 113. *E. angusticollis angusticollis* Sahlberg. 114. *E. viridis* Horn. 115. *E. lheritieri* Antoine. 116. *E. parviceps* Van Dyke. 117. *E. americanus* Dejean, George Lake, Alberta. Figs. 118–121. Elytral pits on interval 3 (right) and 5, discal portion. 118. *E. lapponicus obliteratus* Mannerheim. 119. *E. uliginosus* Fabricius. 120. *E. pyrenoeus* Motschulsky. 121. *E. lindrothi* n. sp.



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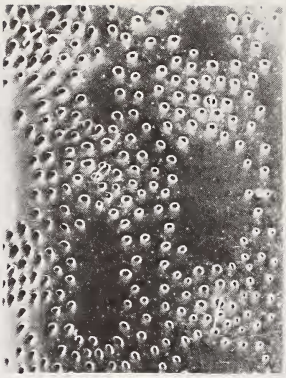

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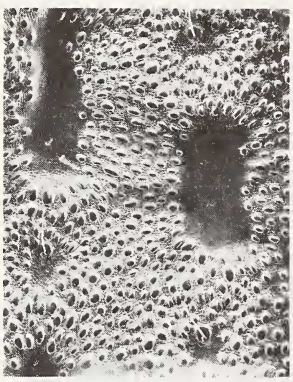

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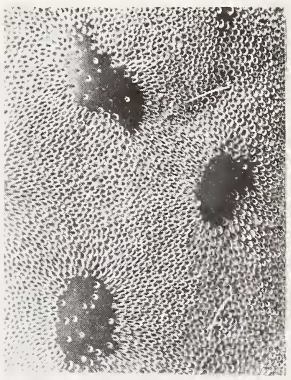

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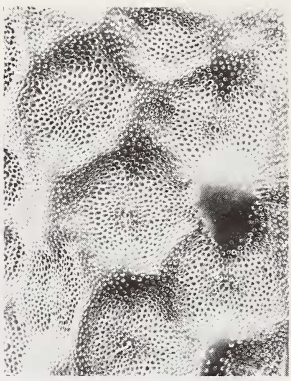

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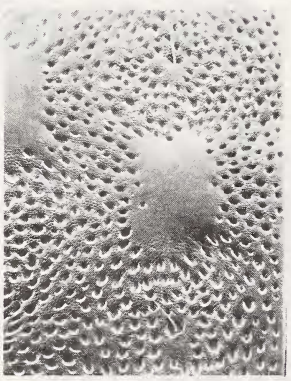

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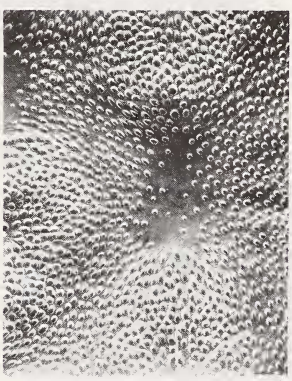
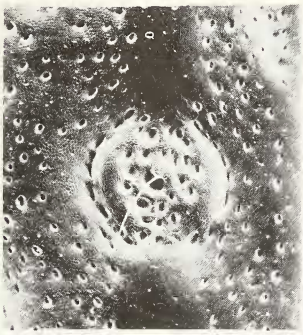


130

Figs. 122–130. Scanning electron micrographs of elytral pits on interval 3 (right) and 5, discal portion of adult Elaphrini. 122. *E. clairvillei* Kirby, George Lake, Alberta. 123. *E. olivaceus* LeConte. 124. *E. punctatus* Motschulsky, Japan. 125. *E. angusticollis angusticollis* Sahlberg. 126. *E. viridis* Horn. 127. *E. lheritieri* Antoine. 128. *E. americanus* Dejean, George Lake, Alberta. 129. *E. parviceps* Van Dyke. 130. E. *lecontei* Crotch, Pakowki Lake, Alberta.

131



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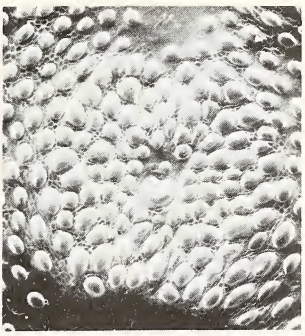

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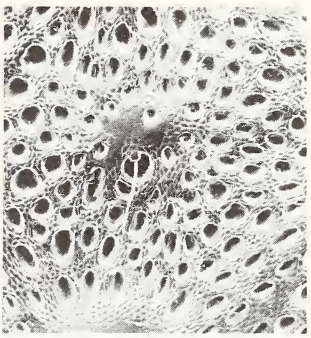

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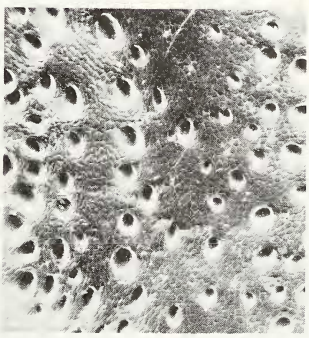

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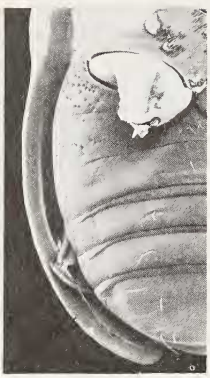
Figs. 131–138. Scanning electron micrographs of elytral sculpture of adult Elaphrini. Figs. 131–136. First sutural pit of elytron. 131. *E. lapponicus obliteratus* Mannerheim. 132. *E. cupreus* Duftschmid. 133. *E. clairvillei* Kirby. 134. *E. olivaceus* LeConte. 135. *E. americanus* Dejean, George Lake, Alberta. 136. *E. parviceps* Van Dyke. Figs. 137–138. Microsculpture on elytral interval 4. 137. *E. uliginosus* Fabricius. 138. *E. pyrenoeus* Motschulsky.



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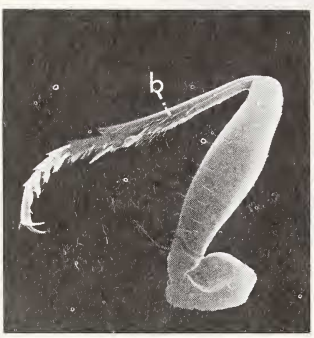

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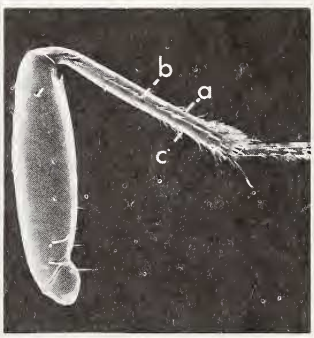

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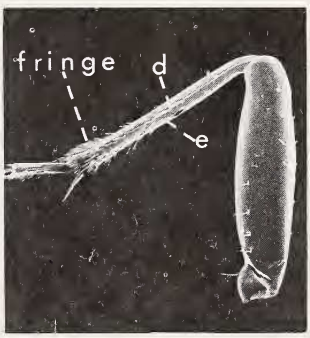
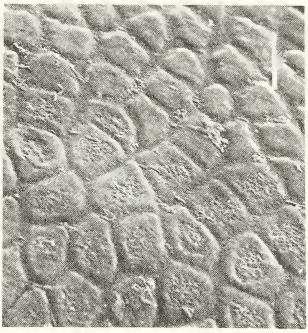


148

Figs. 139–148. Scanning electron micrographs of abdominal sterna and legs of adult Elaphrini. Figs. 139–142. Abdominal sterna. 139. *E. cicatricosus* LeConte. 140. *E. californicus* Mannerheim. 141. *E. riparius* Linnaeus. 142. *E. parviceps* Van Dyke. Figs. 143–144. Microsculpture on abdominal sterna 4 and 5. 143. *E. riparius* Linnaeus. 144. *E. parviceps* Van Dyke. Figs. 145–146. Foreleg of *E. cicatricosus* LeConte. 145. Anterior aspect. 146. Posterior aspect. Figs. 147–148. Midleg of *E. cicatricosus* LeConte. 147. Anterior aspect. 148. Posterior aspect.

149

150



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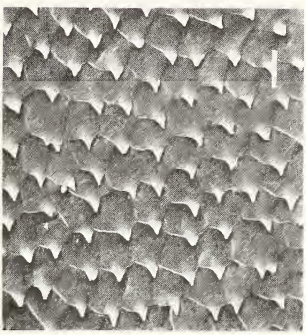


153

154

155

156

Figs. 149–156. Scanning electron micrographs of structures of Elaphrini. Figs. 149–150. Male adults of *E. cicatricosus* LeConte. 149. Apex of foreleg, posterior aspect. 150. Apex of midleg, posterior aspect. Figs. 151–156. Types of microsculpture (scale bar = 10 microns). 151. Isodiametric microsculpture, upper half smooth, lower half punctate (brown areas)– based on third instar larva of *E. angusticollis angusticollis* Sahlberg. 152. Scale-like microsculpture on side of head of third instar larva of *E. angusticollis angusticollis* Sahlberg. 153. Sharp scale-like microsculpture on abdominal sterna of adult *E. riparius* Linnaeus. 154. Single, double and triple-pointed microsculpture on tergum of third instar larva of *E. californicus* Mannerheim. 155. Raised multipointed microsculpture on abdominal sternum of third instar *E. californicus* Mannerheim. 156. Fine multi-pointed microsculpture on abdominal epipleuron of third instar larva of *E. angusticollis angusticollis* Sahlberg.

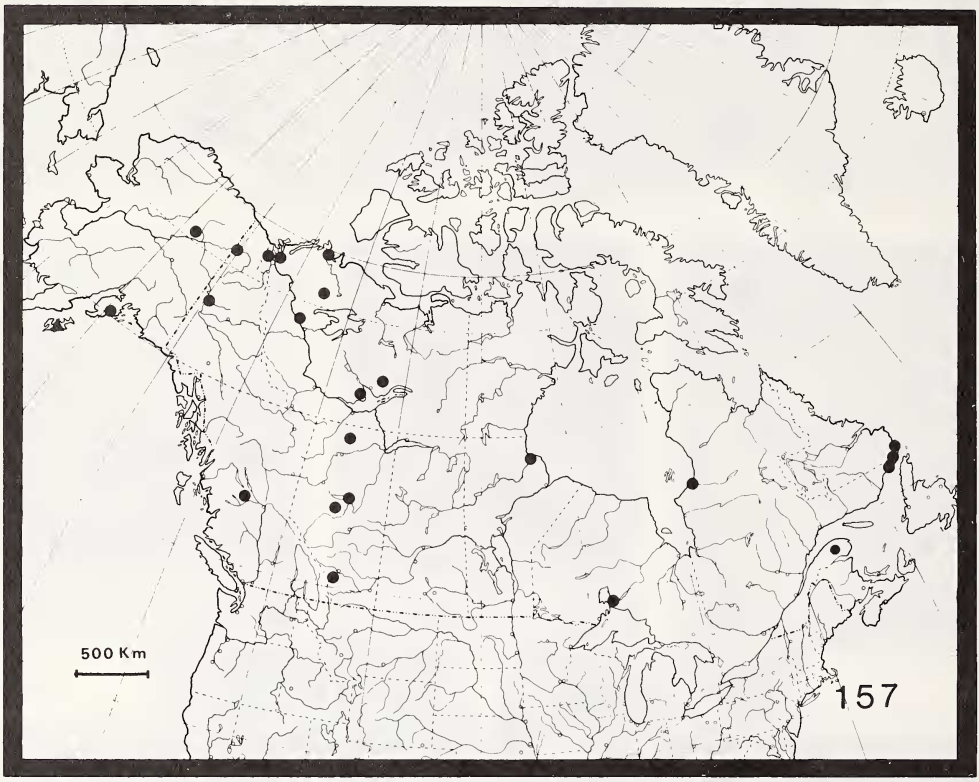
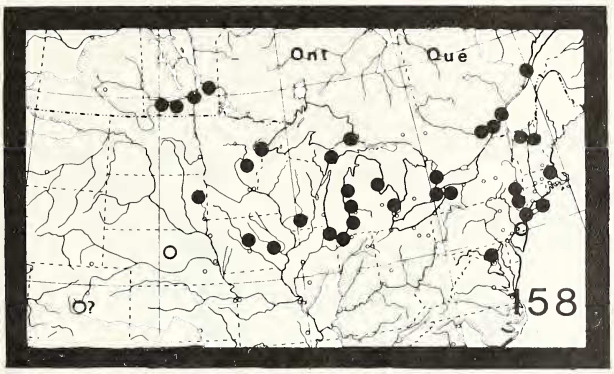
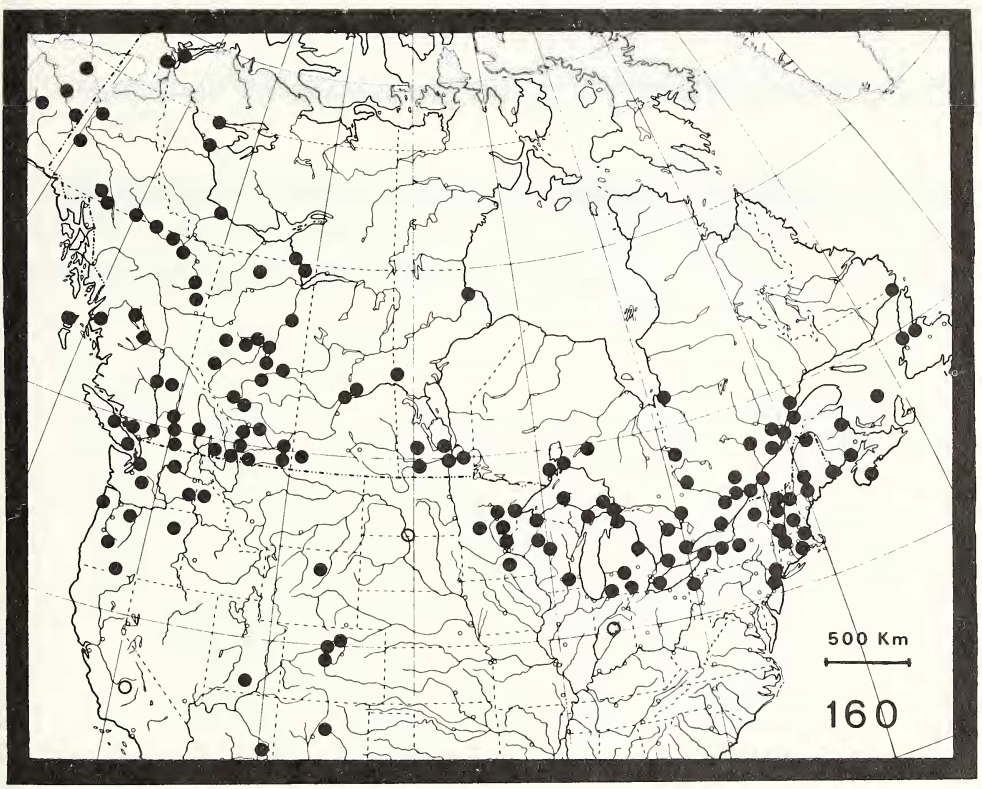
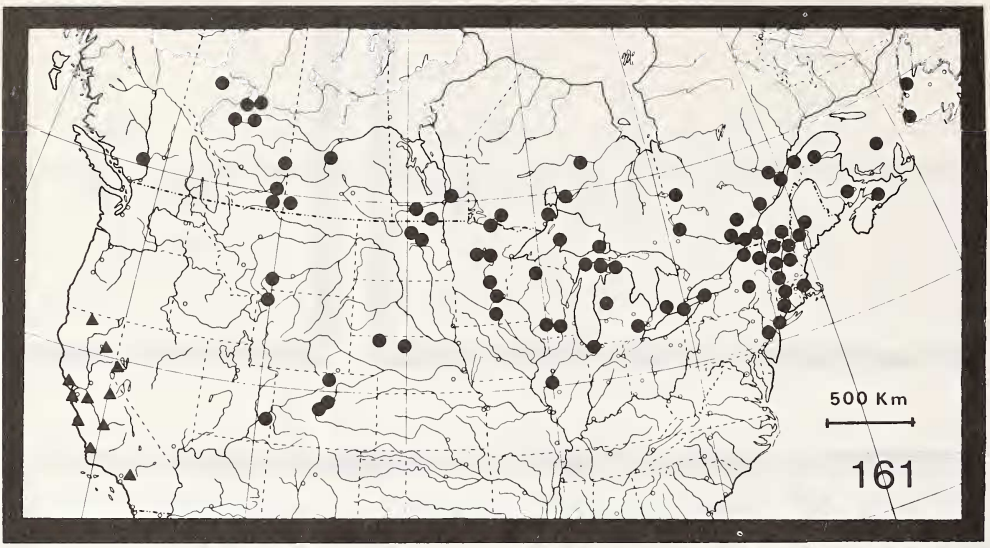


Fig. 157. Known distribution of *E. lapponicus lapponicus* Gyllenhal (circles) and *E. l. obliteratus* Mannerheim (traingle) in North America.





Figs. 158–160. Known distribution. 158. *E. fuliginosus* Say. 159. *E. cicatricosus* LeConte (circles), and *E. lindrothi* n. sp. (triangles). 160. *E. clairvillei* Kirby.



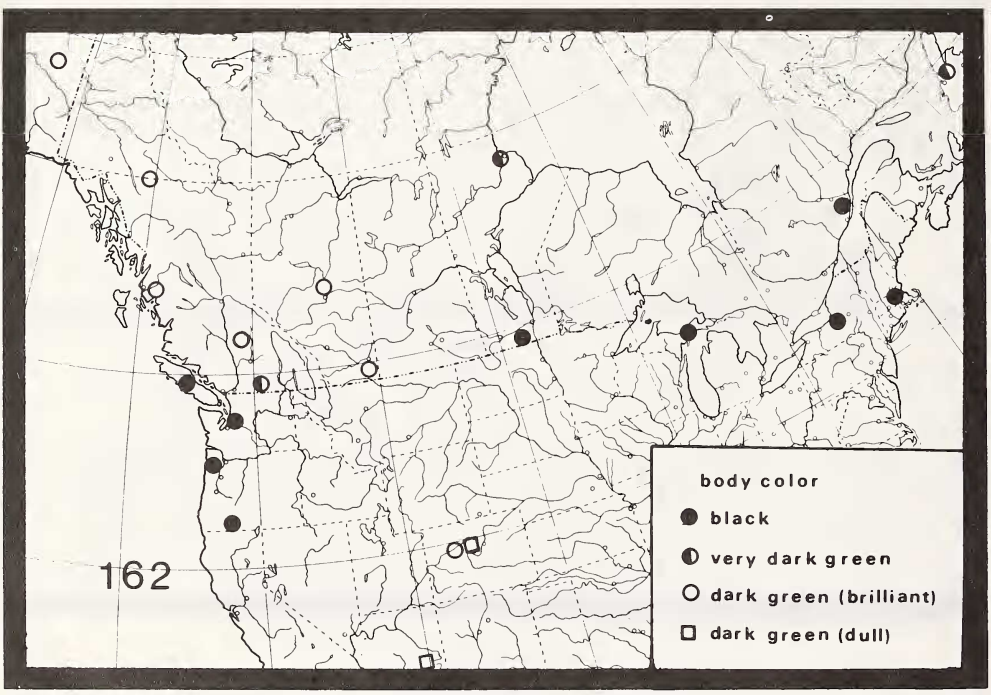
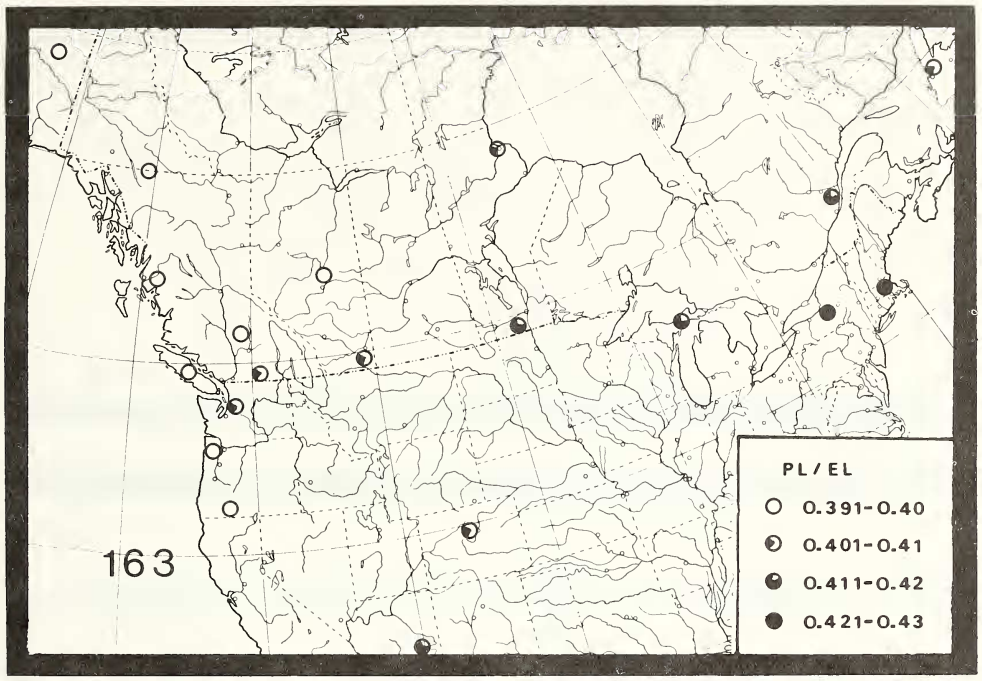
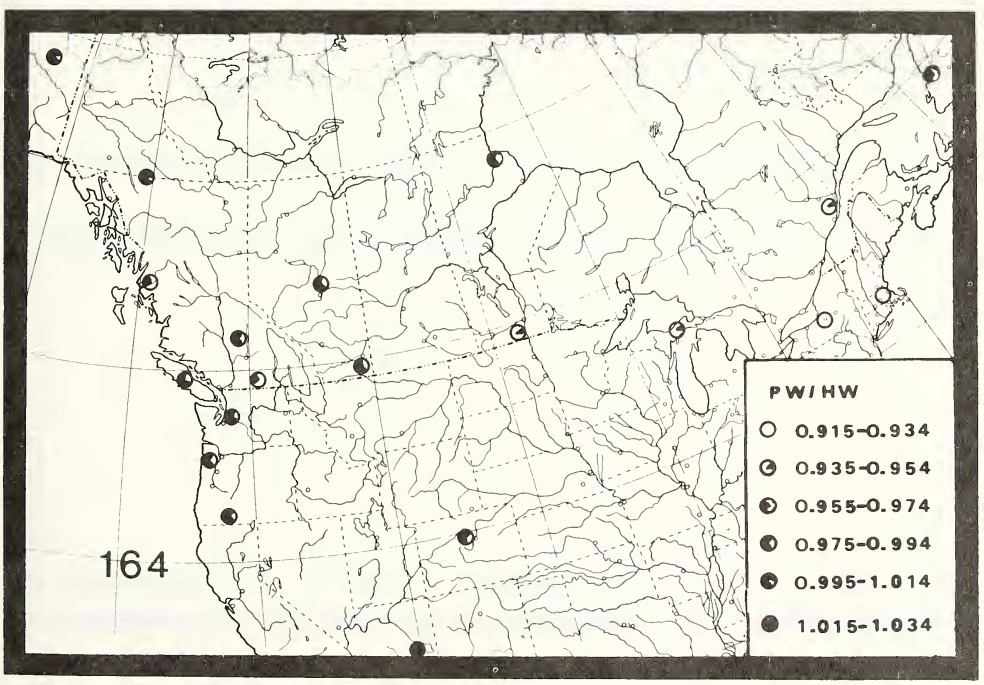
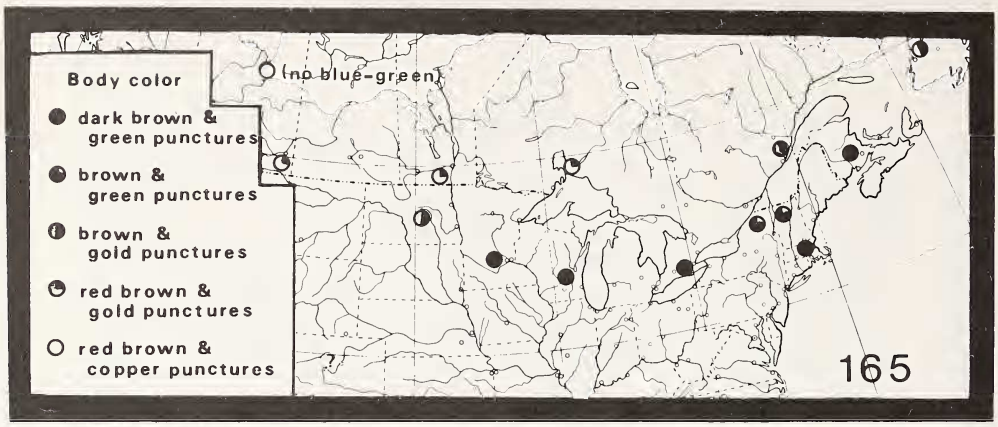


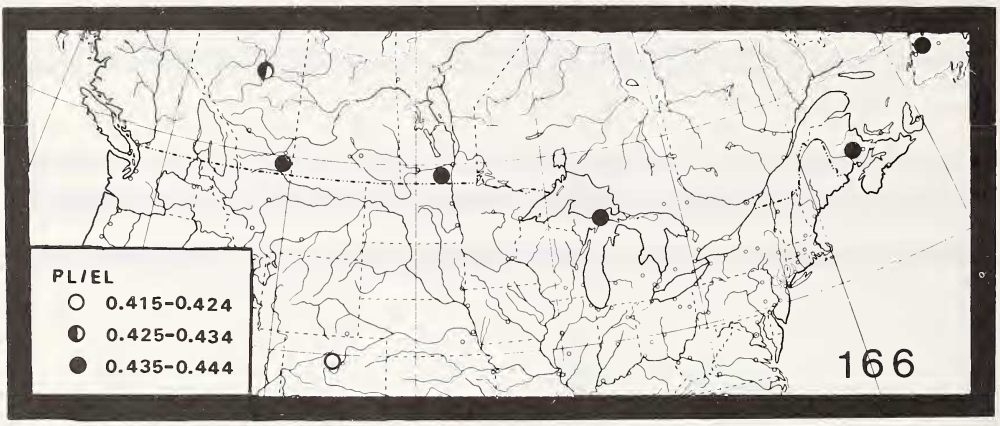
Fig. 161. Known distribution of *E. olivaceus* LeConte (circles) and *E. laevigatus* LeConte (triangles). Fig. 162. Variation in dorsal color of adults of *E. clairvillei* Kirby.

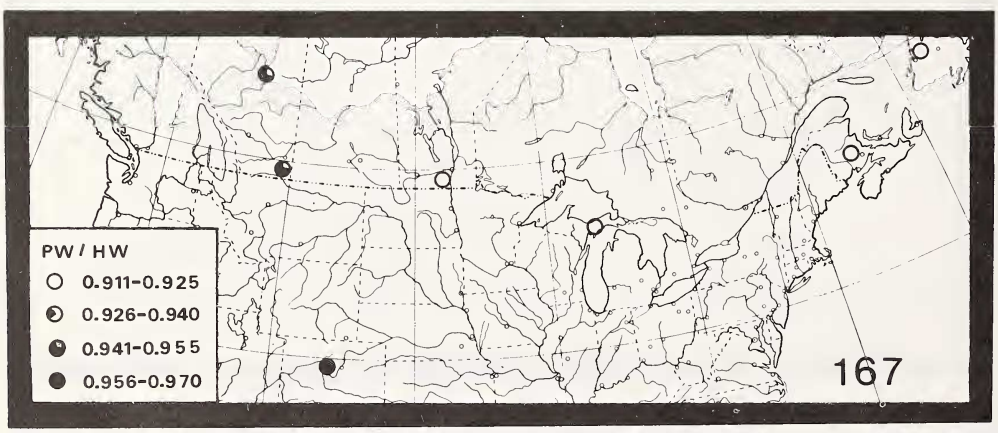




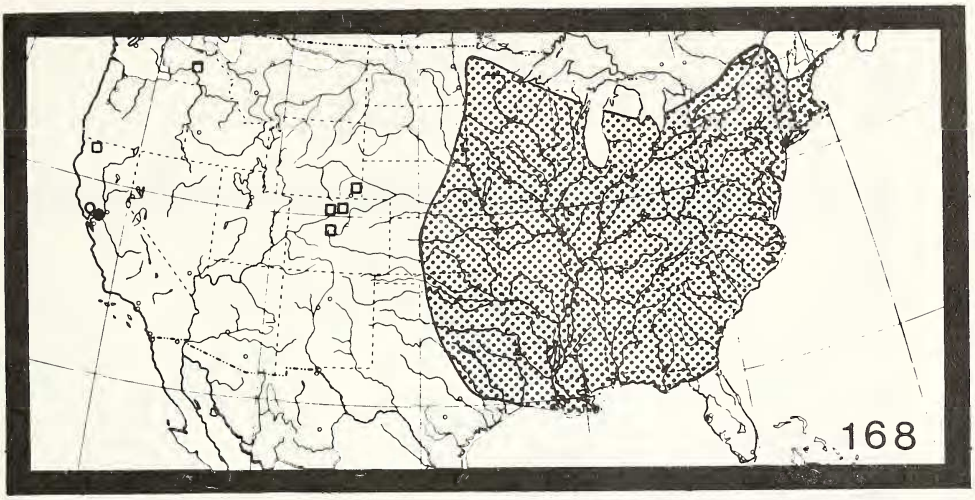
Figs. 163–164. Variation, based on adults of *E. clairvillei* Kirby. 163. Ratio PL/EL. 164. Ratio PW/HW.

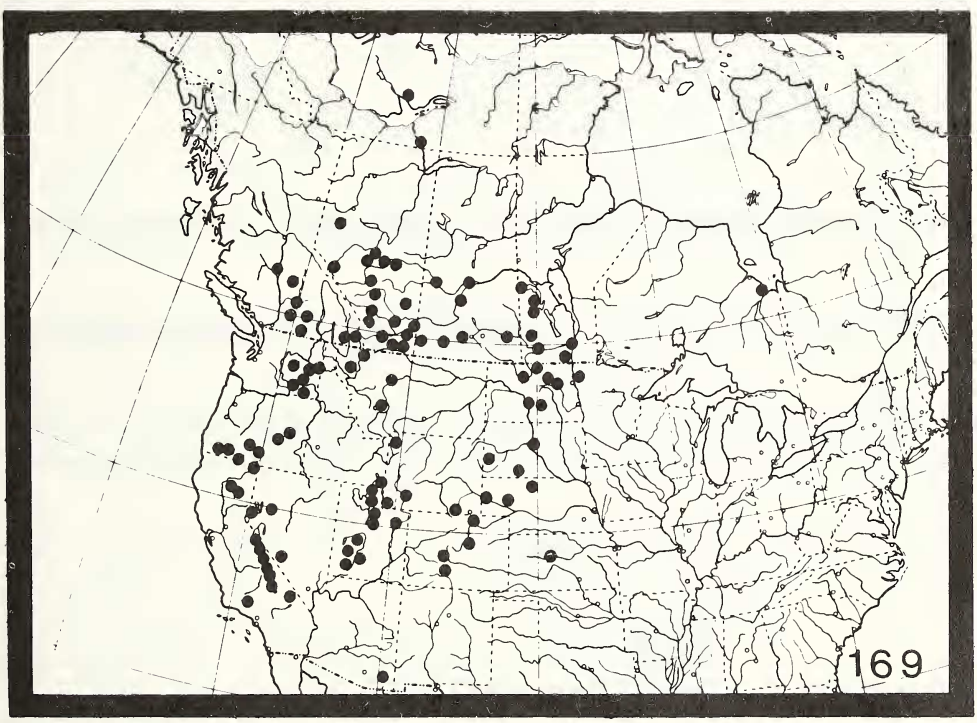






Figs. 165–167. Variation, based on adults of *E. olivaceus* LeConte. 165. Variation of dark form. 166. Ratio PL/EL. 167. Ratio PW/HW.





Figs. 168–169. Known distribution. 168. *E. marginicollis* n. sp. (open squares), *E. mimus* n. sp. (open circle), *E. viridis* Horn (black circles), and *E. ruscarius* Say (stippled surface). 169. *E. lecontei* Crotch.

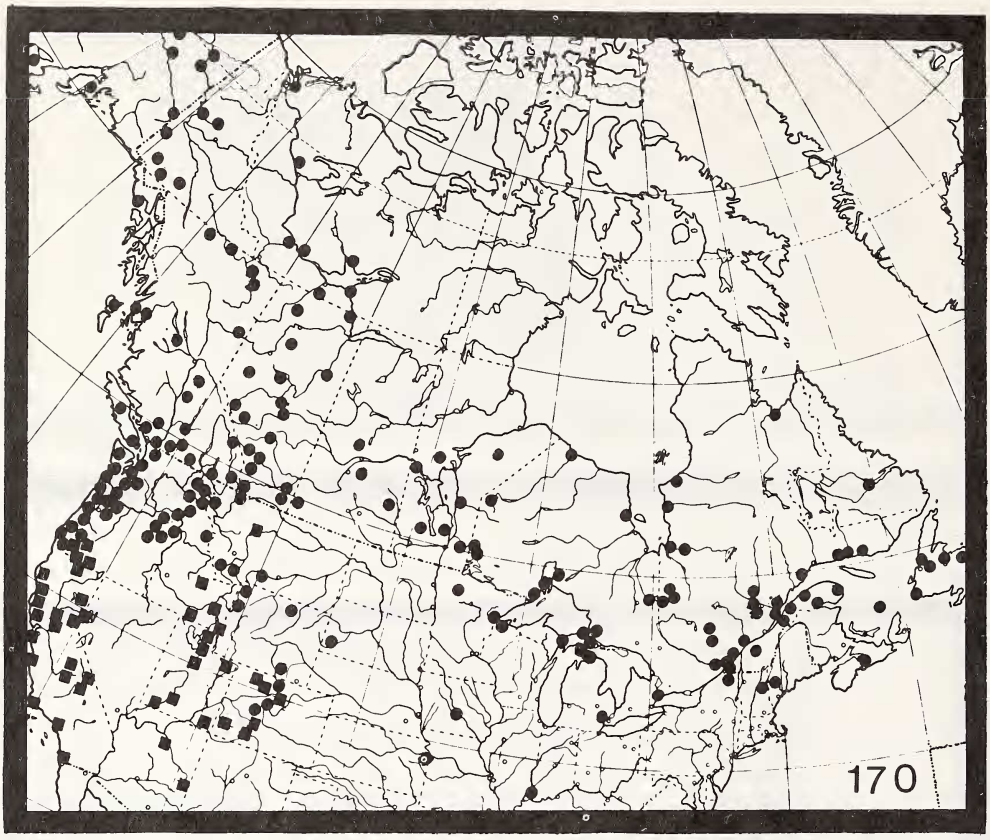
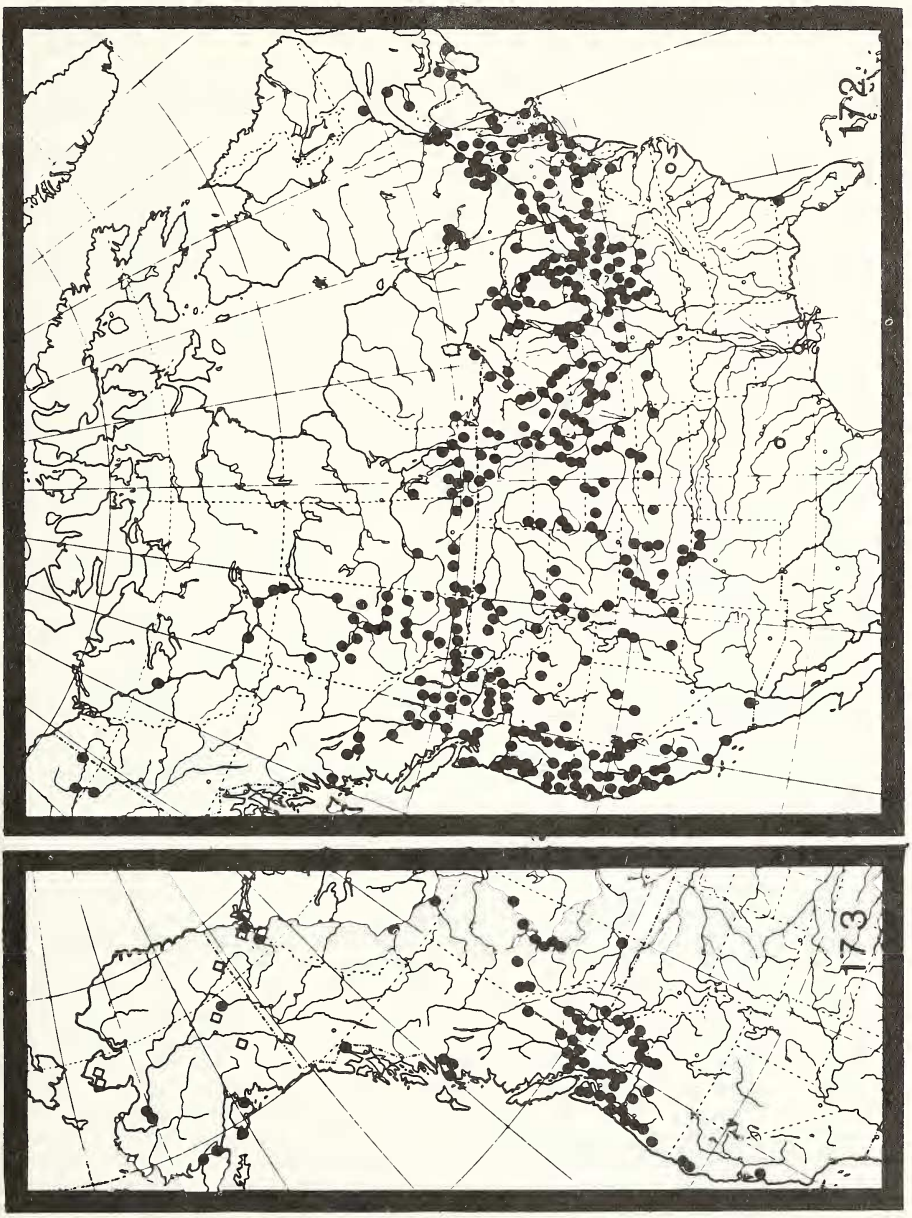


Fig. 170. Known distribution of *E. americanus* Kirby (circles) and *E. finitimus* Casey (squares). Fig. 171. Known Nearctic distribution of *E. tuberculatus* Mäklin (squares) and *E. parviceps* Van Dyke (circles).



Figs. 172–173. Known distribution. 172. *E. californicus* Mannerheim– state records noted as open circles. 173. *E. purpurans* Hausen (black circles) and *E. angusticollis angusticollis* Sahlberg (open squares).

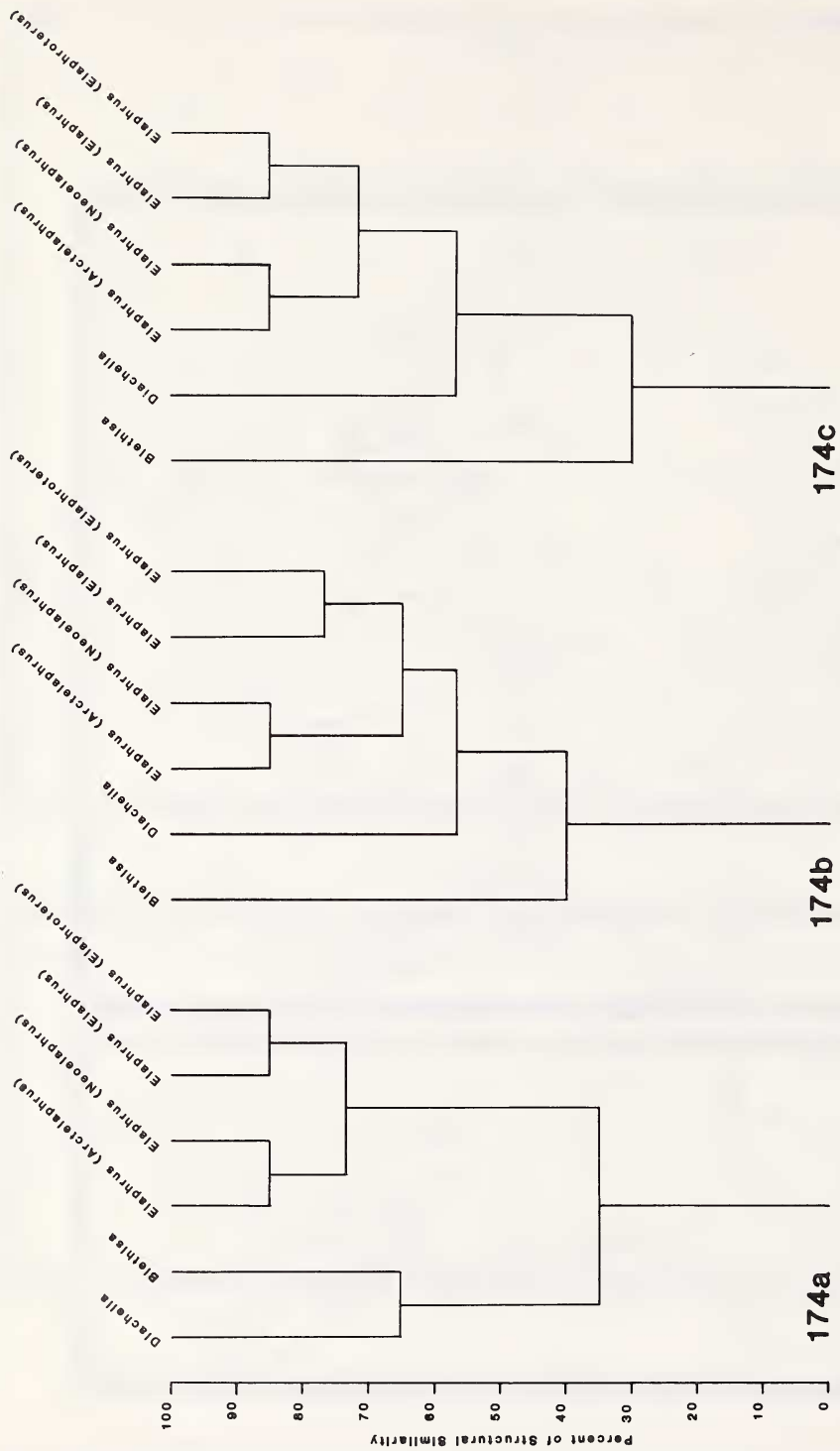


Fig. 174. Phenetic relationships of genera and subgenera of Elaphrini based on a) adults, b) first instar larvae, and c) second instar larvae. See Tables 48 and 49.

NOTES ON STRUCTURES CORRELATED WITH CRYPTIC COLORATION OF ADULTS OF *ELAPHRUS* WITH THEIR SUBSTRATE

It is striking to observe how adult *Elaphrus* match the substrate on which they live. Adults are cryptically colored, and behave in peculiar ways for carabids to enhance their blending with the environment.

I cannot explain the functional significance of most character states studied. However, many structural features seem correlated with cryptic coloration of adults. Indeed, structural details of dorsal coloration lead quite accurately to the habitat of each species. The structures discussed below are: microsculpture, punctures, elytral pits, mirrors, and color. Most examples are of Nearctic species or Nearctic populations of Holarctic species.

Microsculpture. Meshes of microsculpture on the dorsal surface of adults are isodiametric, and sculpticells flat, convex or scale-like. The lack or presence of different types of sculpticells affects the reflected light: lack of sculpticells produces a brilliant surface; presence, especially when sculpticells are convex or scale-like, produces a dull surface. There is a marked correlation between microsculpture of the integument and surface moisture of the substrate on which the beetles live. Meshes are absent over most of intervals on adults of species living on saturated substrates (*E. pyrenoeus, E. clairvillei, E. olivaceus, E. laevigatus, E. lecontei, E. americanus* and *E. finitimus*), and sculpticells are flat or subconvex on adults of species living on moist but not saturated substrates (*E. uliginosus, E. fuliginosus, E. cicatricosus, E. lindrothi, E. ruscarius* and *E. californicus*), and convex or scale-like on those living on moist and firm, or moist and drained substrates (*E. lapponicus, E. tuberculatus, E. angusticollis, E. purpurans* and *E. aureus*).

Punctures. Probably the combined effect of punctures is to break the sharp outline of body (Ball, pers, comm.). Because punctures in this genus are brightly metallic, the above effect is probably amplified by the flash effect of reflected light. There is a marked correlation between average density of punctures over the dorsal surface and particle size of the substrate. Adults with punctures five to 15 microns apart are on clay (*E. californicus* and *E. lecontei*), those with punctures ten to 20 microns apart on silt, fine organic mud, or small moss carpet (*E. pyrenoeus, E. lindrothi, E. olivaceus* and *E. purpurans*), those with punctures 20 to 40 microns apart are on sand and organic mud (*E. uliginosus, E. fuliginosus, E. marginicollis, E. ruscarius, E. americanus, E. riparius, E. tuberculatus, E. parviceps* and *E. angusticollis*), and those with punctures 50 to 200 microns apart are on coarse organic substrate such as dead leaves or large moss carpet (*E. lapponicus, E. cicatricosus, E. clairvillei* and *E. laevigatus*).

Elytral pits. Pits are variously impressed. There is a marked correlation between degree of impression of pits and roughness of the substrate. Pits are absent from or barely impressed on adults living on smooth substrates (*E. viridis* and *E. lecontei*), sharply but not deeply impressed on those living on moderately rough substrates (*E. fuliginosus E. lindrothi, E. olivaceus, E. ruscarius, E. californicus, E. americanus, E. finitimus, E. tuberculatus, E. purpurans* and *E. angusticollis*), sharply and deeply impressed on those living on rough substrates such as dead leaves (*E. cicatricosus, E. clairvillei,* and *E. laevigatus*).

Elytral mirrors. Mirrors reflect light with a flash effect. They vary in size and number. Mirrors look like reflection of light from water between substrate particles. There is some correlation between mirror development and substrate moisture. Mirrors are anastomosed with even intervals on adults living on saturated substrates (*E. pyrenoeus, E. clairvillei, E. olivaceus* and *E. laevigatus),* isolated and numerous on those living on saturated substrates (*E. lecontei, E. americanus , E. finitimus* and *E. parviceps),* and isolated and few (usually only mirrors of interval 3) on those living on moist substrates (*E. lapponicus, E. lindrothi, E. cicatricosus, E. ruscarius, E. californicus* and *E. tuberculatus*). However, the rule does not hold with adults of *Elaphroterus* which have many mirrors and live on moist but not saturated substrates.

Color. Color of the dorsal surface is the summation of complex blending of above structures with pigmentation and metallic reflection of the surface. In absence of metallic reflections, the surface is black. Depending on proportion of reflected light, metallic reflections may range from a hue to a brilliant flash. Space between punctures is, in adults of most species less brilliant than punctures. Blending of color from punctures and surrounding surface is similar to our blending of points of primary color on color television monitors. Adults match closely the color of the substrate. In most species, adults of one sample may be represented by two or three discrete color forms. The proportion of these color forms is constant locally, or, in some species, over large territory. The less dominant color forms are also cryptic over part of habitat. Copper-colored or brown specimens are cryptic over brown mud (*E. americanus, E. riparius,* and *E. parviceps*), red clay (*E. ruscarius*), red organic mud (*E. lecontei* and *E. americanus*), red or brown mosses (*E. lapponicus* and *E. olivaceus*), and leaf litter (*E. purpurans* and *E. angusticollis angusticollis*). Such association of color forms is probably not random, as observed in large samples of *E. americanus sylvanus* in the subalpine zone in the Cascades where copper-colored adults were markedly more abundant on brown mud than on grass or mosses. However, I do not understand the significance of bicolor adults of *E. californicus* which are less cryptic than common gray-green adults on clay surfaces.

The above discussion clearly stresses the amazing complexity of cryptic coloration in adults of *Elaphrus*. The above hypotheses were tested quite successfully in rediscovering adults of rare species (*E. lindrothi, E. viridis, E. tuberculatus, E. parviceps* and *E. angusticollis*), or in forecasting the habitat of some European species (*E. uliginosus, E. pyrenoeus* and *E. cupreus*) before I studied published information.

Cryptic coloration in this genus is an unusual example of trends in a functional complex which could induce systematists into errors about relationships. Indeed, unrelated species pairs living in similar habitats (*E. uliginosus-fuliginosus, E. pyrenoeus-olivaceus, E. clairvillei-leavigatus, E. lindrothi-ruscarius, E. ruscarius-riparius, E. americanus-riparius, E. tuberculatus-angusticollis*) have achieved remarkable parallelisms.

PHENETICS AND CLADISTICS: LARVAE AND ADULTS

In the following discussion, I establish relationships of the genera and subgenera of Elaphrini using separately the procedures of phenetic and cladistic methods. The purpose is to compare results between both systems and to test each system for congruency of results based on adults and larvae. Therefore four systems of relationships will be presented: two phenetic systems, one for adults and one for larvae; and two cladistic systems, one for adults and one for larvae.

Phenetic Association

Numerical methods.— In this analysis, I used any character with states distributed uniformly within genera and subgenera and excluded characteristics restricted to species level. For each character, I coded the states between zero and one. A coded value of this character was attributed to each taxon. Then the coded value of the character for each taxon was compared to that for each other taxon. If the state for two taxa was similar, I recorded zero; if the values of two states were different, I subtracted one from the other and retained the result as an absolute value. If a character was expressed in a higher taxon as two or more states, the numerical values of these states were added and divided by the number of states in this taxon. This was done for all characters. Finally, the absolute differences of all characters for all possible pairs were summed. The result was divided by the number of characters and expressed as a percent of similarity. The results were then expressed as a phenogram. The index of dissimilarity is expressed as follows:

Index of dissimilarity in percent - $1/N(\sum_{i=1} |X_{ij}-X_{il}|)x100$

X - state value of character "i"for taxa "j"and "l"

N - number of characters used.

Results of numerical classification of adults and larvae.— Tables 48 and 49 show the coded values and distribution for each character state. Phenograms for adults and larvae are provided in Fig. 174. At the generic level, adults of *Blethisa* and *Diacheila* are more similar (64%) than they are to those of *Elaphrus* (35%) (Fig. 174a). Based on adults, the four subgenera of *Elaphrus* form two groups of two subgenera each. Adults of *Arctelaphrus* are more similar to those of *Neoelaphrus* (85%) than to those of other subgenera. Adults of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (85%) than to those of other subgenera.

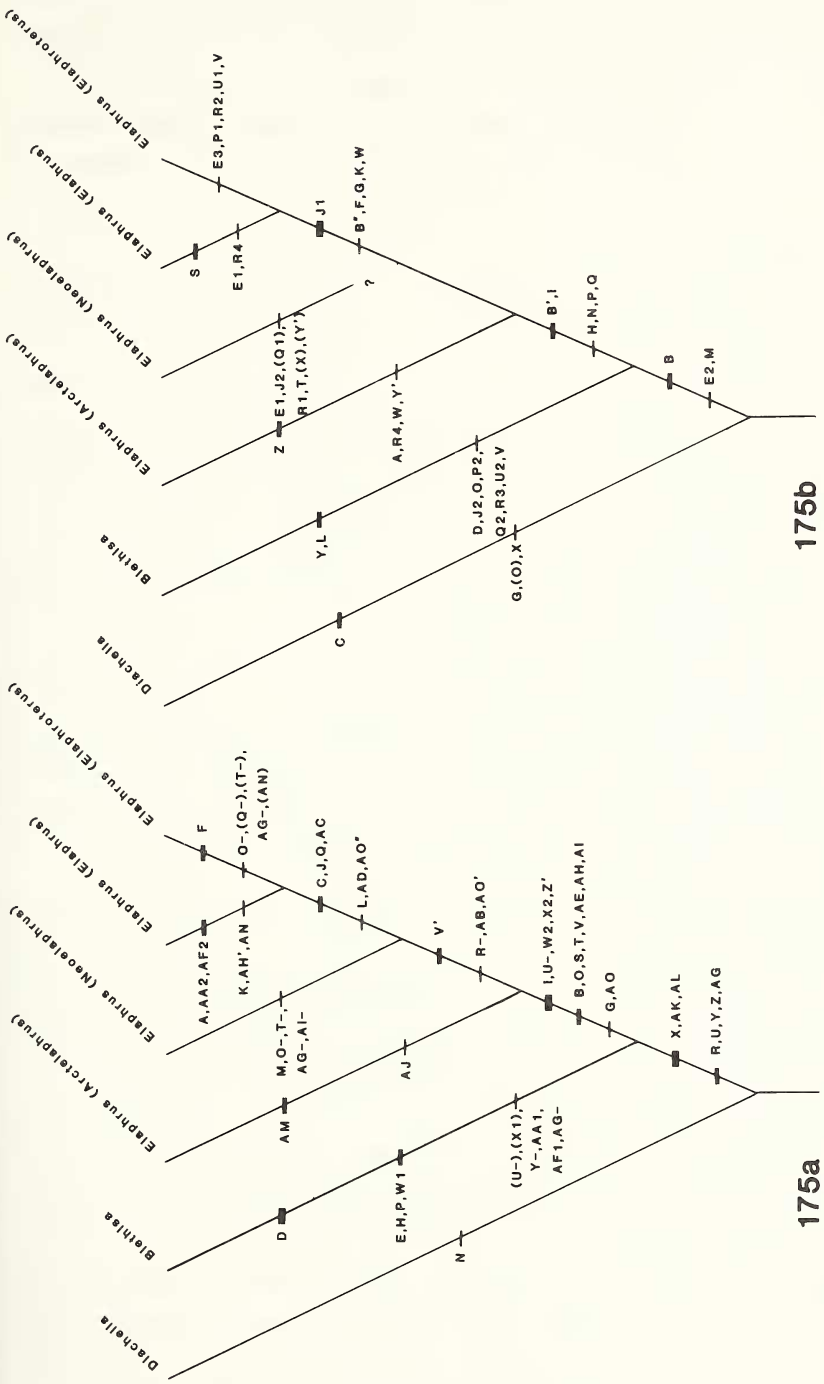


Fig. 175. Reconstructed phylogeny of genera and subgenera of Elaphrini based on a) adults, and b) first, second, and third instar larvae. Capital letters refer to derived states of coded characters (see Tables 50 and 51). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

At the generic level, larvae of *Diacheila* and *Elaphrus* are more similar (57% for first instar larvae, 59% for second instar larvae) than both are to those of *Blethisa* (39% for first instar larvae, 27% for second instar larvae) (Figs. 174b, 174c). Based on larvae, the four subgenera of *Elaphrus* form the same groups of two subgenera each as those based on adults. Larvae of *Arctelaphrus* are more similar to those of *Neoelaphrus* (86% for first instar larvae, 85% for second instar larvae) than to those of other subgenera. Larvae of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (76% of character states of first larvae, 86% of second instar larvae) than to those of other subgenera.

Phylogenetic Association

Cladistic methods.— Hennig (1966), Kavanaugh (1972 and 1978), Whitehead (1972), and Hecht and Edwards (1977) describe the general principles of phylogenetics followed by me. Here, briefly, is the working method I used.

Evolutionary relationships of taxa are determined by recognition of sister taxa. Two or more taxa are likely to share a common ancestor, if they share a derived state of a character (Hennig's (1966) synapomorphic character states). Such group is monophyletic, if it includes all taxa descendant from one common ancestor. A phylogeny is reconstructed step by step, with progressive recognition of sister groups, until all taxa are studied and thus assigned.

Determination of character states polarity.— The main problem is to recognize a derived state (Hennig's (1966) apomorphic state) from an ancestral one (Hennig's (1966) plesiomorphic state). Ross (1974), Ball (1975), Hecht and Edwards (1977) summarize the usual approaches. Basically, out-group comparison is used.

Out-group comparisons.— If the state of a character, expressed in some members of a taxon studied, occurs among taxa of at least the next higher category, then it is likely an ancestral trait. This is based on the assumption that its extensive distribution is the result of inheritance, not of independent evolution. However, as pointed out by Ekis (1977), a state originally widespread among taxa, following massive extinction, may be sparsely distributed among surviving taxa and the existance of relict taxa should be carefully considered when using this type of evidence.

Weighting of character states.— After the polarity of states of one or more characters was decided, I evaluated the weight of each derived state. Some states are of little value since they are likely to have evolved more than once (problems of parallelism and convergence), while other states are so complex or unusual that it is not likely they would have evolved twice in exactly the same structural details. Thus, it is important to select character states of highest weight for phylogenetic reconstruction. Hecht and Edwards (1977) suggested five classes, but I used only three in this work since two of their classes (Hecht and Edward's class 2 and 3) were not observable or applicable.

In the first class, I included character states showing linear variation (*i.e.*, length of setae and density of punctures) and lost states (*i.e.*, loss of setae, sculpture and pigment). This class, termed "1,"is of lowest weight, as reversals and convergent evolution are likely and difficult to detect.

In the second class, I included modified states of simple structures (eg. development of peg-like structure at bases of inner spurs of mid-tibiae of males, and puncture distribution pattern on pronotum.) This class, termed "2", is of moderate weight as reversals and convergences are likely to be detected and their occurrence rare.

In the third class I included new and complex character states (*i.e.,* the complex elytral mirror and pit system in *Elaphrus* , and the complex and integrated stridulatory structures of Elaphrini). This class, termed "3", is of highest weight, as reversals and convergences are most unlikely and would probably be easily detected in an analysis of structural details.

Phylogenetic reconstruction.— Sister groups are recognized by shared possession of a derived state of one or more characters. Reconstruction is done in steps. First, groups are assembled with character states of highest weight, then reconstruction with those of moderate weight, and finally with those of lowest weight. However, the entire phylogeny is not completely reconstructed on character states of high weight, but in part on those of lower weight when those of high weight are not available (see Fig. 178). The law of parsimony is not considered except with character states of lowest weight.

Results of phylogenetic reconstruction.— Data presented in tables 50 to 59 were used in reconstruction of the phylogenetic diagrams (Fig. 175). In these tables, each character was coded by one letter or a combination of two letters. The derived state was represented by capital symbols. Where three or more states were present, and the two or more derived states arose independently, an integer for a lost state was added to the letter code. If the states were part of a morphocline, I used ("), (') , etc. after the letter code, suggesting a clinal progression. The estimate of weight was expressed as "1" for lowest weight, "2" for moderate weight, and "3" for high weight. Out-group evidence in relation to elaphrine beetles was derived from numerous tribes of carabids: Trachypachini, Metriini, Omophronini, Carabini and Nebriini (assumed to be older lineages); and Trechini, Pterostichini, Agonini, Anisodactylini and Harpalini (assumed to be younger lineages). The justifications in determining polarities of character states are summarized in Table 60.

At the generic level, results of analyses of relationships among adults show that *Elaphrus* shares a common ancestor with *Blethisa,* and that both of these genera share a common ancestor with *Diacheila* (Fig. 175a). At the subgeneric level, *Elaphrus* and *Elaphroterus* share a common ancestor, *Neoelaphrus* shares a common ancestor with the above subgenera, and *Arctelaphrus* shares a common ancestor with the above three subgenera.

At the generic and subgeneric levels, relationships among larvae are similar to those described above for adults (Fig. 175b). However, I failed to show the relationships of *Neoelaphrus* relative to *Arctelaphrus.*

Comparisons Between Systems of Association

The three genera were paired three ways by the cladograms and the phenograms: one system based on phenetic relationships of adults gave one result, one based on phenetic relationships of larvae gave another, and one based on phylogentic relatiohships of adults and larvae gave a third. Therefore, the phenograms, based on adults and larvae are incongruent while the cladograms, based on adults and larvae, are congruent.

The subgenera of *Elaphrus* were associated similarly in phenograms based on adults and larvae and in cladograms based on adults and larvae. However, the relationships of *Neoelaphrus* were different between phenograms and cladograms. In phenograms, *Neoelaphrus* was associated with *Arctelaphrus;* while in cladograms, based on adults, *Neoelaphrus* was the sister group of the *Elaphrus-Elaphroterus* group and *Arctelaphrus* was the sister group of all three subgenera.

The phylogenetic reconstruction based independently on adults and larvae was congruent. However, the cladogram based on larvae was difficult to construct since the evidence of

character state distribution was limited (most previous descriptions of larvae are superficial and hence do not provide data needed for analyses of relationships).

Three genera can be paired only three ways. Numerical analysis produced two systems: *Blethisa* and *Diacheila* most similar for adults and *Diacheila* and *Elaphrus* most similar for larvae. The phylogenetic results based on adults and larvae suggested that *Blethisa* and *Elaphrus* are more closely related.

Conclusions

Numerical analysis.— The incongruent results between adults and larvae in the numerical analysis can be explained by various factors: insufficient data, incorrect numerical technique, incorrect coding of states and appropriateness of concept.

In statistical work one expects to approach the real mean as sample size increases. How many characters are necessary to reach consistent results? In my first analysis of adults (based on one *Diacheila,* two *Blethisa* and 13 *Elaphrus* species), I used 288 characters. The results obtained were consistent at the generic level with classifications based on 88 characters from the thoracic and abdominal pleura and sterna, on 57 characters from the head and the tergites, on 51 characters from the dorsum of the head, the pronotum and the elytra, and on 87 characters from the legs. The only discrepancy was at the subgeneric level of genus *Elaphrus* where *Arctelaphrus* was marginally associated with subgenus *Elaphrus* for leg characters. Therefore, in using 80 to 120 characters in analyses of adults and larvae, I probably had enough characters.

I used the simplest index of similarity. More complex cluster analysis techniques are available. However, the taxa compared are very distinct. Therefore, I do not suspect major differences due to techniques for the association of these genera.

Coding can be criticized since for about 40% of characters used, more than two states were found. However, I obtained similar results using only two-state characters in subanalyses of adults and larvae.

Since I probably used enough characters in these analyses, and satisfactory methods, I feel that incongruent results between genera, based on adults and larvae, suggest that something fundamental is missing in the formulation of taxa association.

Pheneticists measure gaps (percent of similarity) between taxa (OTU's of Sokal and Sneath, 1963). Gaps are caused by two factors: extinction of intermediate taxa, and evolutionary rates. The extinction effect, though important in the classification process, is not important in working out relationships. However, evolutionary rates are probably the most important factor explaining incongruent results.

If species are evolving at similar rates at any stage, the overall changes should be less among recently evolved taxa than among those that are older. Therefore, pheonograms based on different stages not only would be congruent but would be a phylogenetic reconstruction. However, evolutionary rates are not only different between species at any stage but these rates are not correlated between stages of the same species.

Since evolutionary rates are not uniform, phenograms, based on different stages, are likely to be incongruent. Phenograms reflect a mixture of effects due to evolutionary rates and recency of descent. Fast-evolving taxa are likely to be singled out (e.g. adult *Elaphrus* or larval *Blethisa*), and slow evolving taxa are likely to be associated (*e.g. Diacheila* and *Blethisa* as adults, and *Diacheila* and *Elaphrus* as larvae). Therefore, the principle of assembling living things based on overall similarity using equally weighted characters is not likely to formulate a

consistent phylogenetic hypothesis. The method used is a measure of distinctness and should not be used for purposes of phylogenetic reconstruction.

Cladistic analysis.— The phylogenetic reconstructions, based separately on adults and larvae, are congruent despite different evolutionary rates between species of each stage and uncorrelated evolutionary rates between stages. Some of the evidence shown to unite *Blethisa* to *Elaphrus,* based on adults and larvae, is based on high weight character states. Therefore, I feel that the cladistic reconstruction is the one that is most likely to provide an evolutionary hypothesis.

Table 48. Distribution of characters of adults among genera and subgenera and of coded character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
Eye *shape:*						
small, 0						
typical, 0.5						
prominent, 1.0	0.25	0.5	1	1	1	1
thickness, cornea:						
similar, 0						
thinner ant., 1.0	0	0	0	0	1	1
Head, *punctures distribution:*						
restricted or absent, 0						
on all of disc, 1.0	1	0	1	1	1	1
Antennae, *proportions, antennomeres 1:2:*						
2x longer, 0						
1.5 to 1.7x longer, 1.0	0	0	1	1	1	1
Mandible, *right, retinacular basal tooth:*						
single, 0						
double, 1.0	0	0	1	1	0	0
retinacular apical tooth:						
near terebral tooth, 0						
distant, 1.0	1	0	1	1	0	0
Maxilla, *proportions palpomeres 3:4:*						
0.67, 0						
0.5, 0.5						
0.3, 1.0	0	0.5	0.5	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
lacinia, teeth size:						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
Labium, *proportion, palpomeres 1:2:*						
0.5, 0						
0.7–0.8, 1.0	1	0	1	1	1	1
Mentum, *no. setae:*						
2, 0						
4, 1.0	0	1	0	0	0	0
Gula, *no. setae:*						
8, 0						
6, 1.0	0	0	0	0	0	1
Thorax, *pronotum, no. lateral setae:*						
2, 0						
1, 1.0	0	0	1	1	1	1
no. discal impressions:						
0, 0						
1 or more, 1.0	0	0	1	1	1	1
lateral bead:						
complete, 0						
incomplete (sinuation), 0.5						
absent, 1.0	0	0	0.5	0.75	1	1
post. fringe, termination from postero-lateral angle:						
before lat. impr., 0						
in lat. impr., 0.5						
at angle, 1.0	0	0.5	0.5	0.75	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
fringe, seta shape:						
narrow, 0						
scimitar, 0.5						
wide scimitar, 1.0	0.5	0	0.5	0.5	1	0.5
punctures distr., disc:						
very restricted, 0						
on all of disc, 1.0	1	0	1	1	1	1
Proepisternum, *suture epist. and epim.:*						
distinct, 0						
indistinct, 1.0	0.5	0	0	0	1	1
ridge, epist. and flange:						
complete, 0						
0.5 complete, 0.5						
0.05 complete, 1.0	0.5	0	1	1	1	1
flange size:						
small, 0						
medium, 0.5						
large, 1.0	0	0	0.5	1	1	1
Prosternum, *lat. margin shape:*						
angulate, 0						
sinuate, 1.0	0	0	0	1	0	0
ant. fringe, seta shape:						
narrow, 0						
narrow + scimitar, 0.33						
scimitar, 0.67						
wide scimitar, 1.0	0.33	0	0.67	0.67	1	0.67
disc, setae distribution:						
absent, 0						
intercoxal process, 0.5						
covering disc, 1.0	0	0	1	0.25	1	0.25

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
pointed sculpture, cox. cav.						
small points, 0						
large points, 1.0	0	0	1	1	1	1
Scutellum, *basal ridge:*						
present, 0						
absent, 1.0	1	0	1	1	1	1
punctures:						
present, 0						
absent, 1.0	0	1	0	0	0	0
Mesepisternum,						
anterior submedial ridge:						
distinct, 0						
absent or indistinct, 1.0	0.5	0	1	1	1	1
Mesosternum, *lateral ridge:*						
distinct, 0						
indistinct, 0.5						
absent, 1.0	1	0	0.5	0.5	1	1
Mesosternum,						
intercoxal process, setae:						
absent, 0						
present, 1.0	0	0	0	0	1	0.5
Metanotum						
size apico-lateral setae:						
large, 0						
small, 1.0	1	0	1	1	1	1
Metepisternum, *ant. ridge:*						
convex ridge, 0						
ridge distinct, 0.5						
absent, 1.0	0.25	0	0.5	0.5	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
Metasternum, *ant. acc. setae:*						
present, 0						
absent, 1.0	1	1	0	0	0	0
lateral setae:						
present, 0						
absent, 1.0	1	1	0	1	0	0.5
Abdomen, terga						
setae, tergum 1:						
absent, 0						
present, 1.0	0	1	0	0	0	0
ant. submedial ridges, tergum 2:						
absent, 0						
present, 1.0	0	0	1	1	1	1
stridulatory scraper, points density:						
20 microns apart, 0						
30–40 microns apart, 1.0	1	0	0	0	0	0
microsculpture, tergum 8:						
absent, 0						
present, 1.0	0.5	0	1	1	1	1
Sterna 3–4, *medial acc. setae:*						
absent, 0						
present, 1.0	0	0.5	1	1	1	1
apical setae, sternum 7:						
2, 0						
4, 1.0	0	1	1	1	1	0.5
puncture distribution:						
sternum 2, 0						
sterna 2–4, 0.5						
sterna 2–6, 1.0	0.5	0	1	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
Elytra,						
striae, disc:						
distinct, 0						
indistinct, 0.5						
absent, 1.0	0	0	0.5	0.5	1	1
transverse basal stria:						
complete, 0						
terminated at stria 5, 0.5						
terminated at shoulder, 1.0	0.75	0.25	1	1	1	1
stria 5, base:						
indistinctly impressed, 0						
deeply impressed, 1.0	0.5	0	1	1	1	1
setigerous punctures, no. discal rows						
1, 0						
2, 0.5						
3, 1.0	0	0.5	1	1	1	1
size:						
20 microns, 0						
30 microns, 0.5						
40–60 microns, 1.0	0	0	0.5	1	1	1
interval 3:						
entire, 0						
catenate, 0.5						
catenation mirror-like, 1.0	0	0.5	1	1	1	1
pits, ridges:						
absent, 0						
narrow, 0.5						
wide, 1.0	0	0	1	0.75	0	0
punctures:						
absent, 0						
3–25, 0.33						

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
30–50, 0.67						
50 or more, 1.0	0	0	0.33	0.33	1	0.67
intervals 4, 6 and 8, punctures:						
present, 0						
absent, 1.0	1	1	0	0	0	0
micropores in punctures:						
few, 0						
regular, 0.5						
common, 1.0	0	0	1	1	0	0.5
elytral articulation no. elongate punctures:						
5–7, 0						
2–4, 1.0	0	0	0	0	1	1
elytral epipl., punctures:						
absent, 0						
present, 1.0	1	0	1	1	1	1
Legs, foreleg, coxa, *punctures:*						
absent, 0						
present, 1.0	1	0	1	1	1	1
trochanter, no. setae:						
1, 0						
2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
fermur, no. setae:						
10–25, 0						
30–60, 0.5						
60–80, 1.0	0	0	1	0.5	1	0.5

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
tibia, male, no. setae:						
15–27, 0						
30–45, 1.0	0	0	0.5	1	1	0.5
fringe, basal setae:						
4–8, 0						
absent, 1.0	0	0	0	1	1	1
setae no., postero-medial row, male:female:						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
tarsomere, male, no. enlarged:						
4, 0						
3, 1.0	0	0	0	0	1	1
Midleg,						
coxa punctures:						
absent, 0						
present, 1.0	0.5	0	1	1	1	0.5
setae no.:						
1 or 2, 0						
numerous, 1.0	0	0	1	1	1	1
trochanter, setae no.:						
absent, 0						
1 or 2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
femur, setae no.:						
30–45, 0						
80–110, 1.0	0	0	1	0.5	1	0.5
antero-medial row apex:						
expanded, 0						
linear, 1.0	0	0	1	1	1	1

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Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
Hind leg,						
coxa punctures:						
present, 0						
absent, 1.0	0.5	1	0	0	0	0
coxa, setae no.:						
2, 0						
3, 0.33						
3–15, 0.67						
30–40, 1.0	0.33	0	0.67	0.5	1	0.67
trochanter, spinules no.:						
4–6, 0						
10–15, 1.0	0	1	0	0	0	0
femur, setae no.:						
1–4, 0						
5–10, 0.5						
15–30, 1.0	0	0	1	0.5	1	1
tibia, external row:						
absent, 0						
present, 1.0	0	0	1	1	1	1
antero-medial row apex:						
expanded, 0						
linear, 1.0	0	0	1	1	1	1
Male genitalia, *median lobe*						
baso-dorsal:						
open, 0						
closed, 1.0	1	0	0	0	0	0
stylet, base:						
narrow, 0						
enlarged, 1.0	0	1	1	1	1	1

(continued on next page)

Table 48 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES					
	D	B	A	N	E	Et
apico-ventral point:						
present, 0						
absent, 1.0	1	0	1	1	1	1
parameres, width, right:left:						
0.75, 0						
0.50–0.3, 1.0	0	0	0	0	1	1
Ovipositor, stylus,						
basal sclerite, setae:						
apical 0.67, 0						
apical 0.25, 0.33						
apical 0.1, 0.67						
absent, 1.0	0.5	0	0.67	0.33	1	1
ridge:						
present, 0						
absent, 1.0	0	1	0	0	0	0
apical sclerite, disc, setae no.:						
many, 0						
few (4–6), 0.5						
absent, 1.0	0.5	0	0.5	0.5	0.5	1
setae size:						
absent, 0						
fine, 0.5						
stout, 1.0	0.5	0.5	1	1	1	0
apical setae, no. and size,:						
2 small, 0						
2 very small, 0.33						
1 very small, 0.67						
absent, 1.0	0	0	0.33	0.67	1	1

Table 49. Distribution of characters of larvae among genera and subgenera and of coded character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	Stage	TAXA AND DISTRIBUTION OF CHARACTER STATES D	B	A	N	E	Et
Head, frontale, nasale,							
medial point:							
slightly prominent, 0							
prominent, 0.33							
very prominent, 0.67							
extr. prominent, 1.0	1–3	0	0.33	0.67	0.67	1	1
teeth distribution:							
united, 0							
separated, 0.33							
very separated, 0.67							
extr. separated, 1.0	1–3	0.16	0	0.33	0.33	1	0.67
teeth size:							
absent, 0							
very small, 0.25							
small, 0.5							
large, 0.75							
very large, 1.0	1	0.5	1	0.75	0.37	0.12	0.05
very small, 0							
small, 0.33							
large, 0.67							
very large, 1.0	2–3	0.33	1	0.67	0.67	0	0.33
position seta MMP-E:							
egg-bursters:							
internal, 0							
external, 1.0	1	0	1	1	1	0	0
pore MA-I:seta MMA:							
internal, 0							
parallel, 1.0	1	0	1	1	1	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
		TAXA AND DISTRIBUTION OF CHARACTER STATES					
seta size, EA-E:							
small, 0							
medium-small, 1.0	1–3	0	1	0	0	0	0.25
EM-P:							
virtually absent, 0							
small, 1.0	1–3	0	1	0	0	0	0
MP:							
virtually absent, 0							
small or larger, 1.0	1–3	0	1	0	0	0	0
Accessory setae *size:*							
absent, 0							
small, 1.0	2–3	0	1	0	0	0	0
Microsculpture							
antero-medially:							
absent, 0							
present, 1.0	2–3	0	1	0	0	0	0
Parietale *shape:*							
elongate, 0							
short, 1.0	1–3	1	0	0	0	1	1
occipital suture:							
0.6–1.2 scape l., 0							
0.2–0.6 scape l., 1.0	1	0	0	0	0	1	1
position, pore DI-P							
140–160°, 0							
120–130°, 0.5							
90–120°, 1.0	1–3	0	0	0.5	0.5	1	1
seta DI–A:							
post. to post.-lat. angle, 0							
level with angle, 1.0	1–3	0	0	0	0	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	TAXA AND DISTRIBUTION OF CHARACTER STATES D	B	A	N	E	Et
seta DMM–P							
level with post.-lat.							
angle, 0							
anterior, 1.0	1–3	0	0	0	0	1	1
seta VEM-P:setae							
DEP and VEP-P:							
distant, 0							
moderate, 0.5							
close, 1.0	1–3	0.75	0.25	0.5	0.5	0.9	1.0
pore VEM-A:seta VEM-P:							
distant, 0							
close, 1.0	1–3	0	0	1	1	1	1
pore VEP-A:seta VEP-P:							
external, 0							
internal, 1.0	1–3	0	0	1	1	1	1
basic seta size, DI-A:							
small, 0							
medium, 0.5							
large, 1.0	2–3	0	1	0.5	0.5	0.5	0.5
DMP-A							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0.5	0.5
very small, 0							
medium, 0.5							
large, 1.0	2–3	0	1	0.5	0.5	0.5	0.5
DEP:							
very small, 0							
medium, 0.33							
large, 0.67							
very large, 1.0	1–3	0	1	0.33	0.67	0.33	0.33

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
VMA:							
small, 0							
medium, 0.5							
large, 1.0	1	0	1	0.5	0.5	0	0
small, 0							
medium, 1.0	2–3	0	1	1	1	1	1
VEP-A:							
medium, 0							
very large, 1.0	1–3	0	1	0	0	0	0
VEM-P:							
small, 0							
medium, 0.5							
large, 1.0	1–3	0	1	0.5	0.5	0.5	0.5
VEP-P:							
medium, 0							
large, 0.5							
very large, 1.0	1–3	0	1	0.5	0.5	0	0
no. accessory setae near DMM system:							
0–5, 0							
7–9, 1.0	2	0	1	1	1	0	1
lateral surface:							
3–4, 0							
5–6, 0.5							
7–9, 1.0	2	0	1	0	0	0	0.5
accessory setae size, between DMM-P and DI-A:							
absent, 0							
small, 1.0	2–3	0	1	0	0	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
			TAXA AND DISTRIBUTION OF CHARACTER STATES				
microsculpture, dorso-laterally: absent, 0 lateral, 0.33 on most, 0.67 on all, 1.0	1	0	1	0.5	1	0.33	0.5
absent, 0 lateral, 0.5 on all, 1.0	2	0	1	1	0	0	0.25
latero-ventrally: absent, 0 latero-basal, 0.5 lateral, 1.0	1	0	1	1	0.75	0.5	0.75
pointed sculpture, dorso-laterally: 0%, 0 1–10%, 0.33 15–30%, 0.67 70%, 1.0	2	0	0.33	1	0.5	0.33	0.5
latero-ventrally: absent, 0 1–5%, 0.5 10–30%, 1.0	1	0	0	0	0.75	0	0.75
absent, 0 3–5%, 1.0	2–3	0	0	0	0.5	0	0.5
Antennae, *proportion, antennomeres 1:2:* 1.5, 0 1.0, 1.0	1	1	0	1	1	1	1
Mandibles, *base width:* narrow, 0 wide, 1.0	1–3	0	0	1	1	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
Maxillary stipes,							
proportion,							
ventral view:							
short, 0							
medium, 0.5							
long, 1.0	1–3	0	1	0	0.5	0	0
lateral surface:							
sclerotized, 0							
with unsclerotized band, 0.5							
unsclerotized band extruded, 1.0	1–3	0.5	0	0.5	0	0.5	1
position,							
interno-basal pore:							
distant, 0							
close, 1.0	1–3	1	0	0	0	1	1
antero-external seta vs lacinia:							
posterior, 0							
anterior, 1.0	1–3	1	1	0	0	0	0
seta size, antero-internal:							
small, 0							
medium, 1.0	2–3	1	0	0	0	0	0
no. accessory setae, postero-external:							
absent, 0							
present, 1.0	2	0	1	0	0	0	0
internal, 0.5, dorsum:							
20–30, 0							
40–50, 1.0	1–3	0	0	0	0	0	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
		TAXA AND DISTRIBUTION OF CHARACTER STATES					
no. rows in apical 0.3:							
1, 0							
2, 0.5							
3 or more, 1.0	1–3	0	0	0	0	0.5	0.75
Lacinia, *shape:*							
conical, 0							
suggested, 1.0	1–3	0	0	1	1	1	1
basic setae size,							
extremely small, 0							
small, 1.0	1–3	0.5	0	1	1	1	1
Galea, *galeomere 2*							
position, internal							
microseta:							
apical 0.6–0.8, 0							
apical 0.6–0.4, 0.5							
apical 0.3–0.1, 1.0	1–3	0.5	0	0.5	0.5	1	1
galeomere 2,							
size basic seta:							
virtually absent, 0							
very small, 0.5							
small or larger, 1.0	1–3	0	0.5	0.5	0.5	1	1
Maxillary palpi,							
proportion,							
palpomeres, 1:2:							
1.5, 0							
1.0, 1.0	1	0	0	0	0	1	1
Labium, *ligula size:*							
wider, 0							
narrower, 1.0	1–3	0	0	1	1	1	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
basic seta size, antero-dorsal:							
small or smaller, 0							
medium-small, 1.0	1	0	0	0	0	0	1
very small, 0							
small, 1.0	2–3	0	1	1	1	1	1
no. accessory setae, dorso-laterally:							
2, 0							
5–6, 0.5							
9–15, 1.0	2	0	1	0	0.5	0.5	1
accessory setae size, baso-laterally:							
small, 0							
medium, 1.0	2	0	1	1	1	1	1
Thorax, pronotum, *basic seta size, MI:*							
very small, 0							
small, 0.5							
medium, 1.0	1–3	0	1	0	1	0	0.5
ME-I:							
very small, 0							
small, 0.5							
medium, 1.0	1–3	0	1	0	1	1	0.5
PII-P:							
very small, 0							
small, 0.5							
medium-small, 1.0	1–3	0	1	0.5	1	0	0.5

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
		TAXA AND DISTRIBUTION OF CHARACTER STATES					
no. accessory setae disc:							
5, 0							
15–20, 0.33							
25–50, 0.67							
90 or more, 1.0	2	0	1	0.33	0.33	0.33	0.67
epipleuron:							
1, 0							
2, 0.33							
3, 0.67							
12–14, 1.0	2	0	1	0.1	0.4	0.1	0.2
accessory setae size, posterior row:							
absent, 0							
small, 1.0	2–3	0	1	1	1	1	1
epipleuron:							
absent, 0							
very small, 0.33							
medium-small, 0.67							
medium-large, 1.0	2	0	1	0.33	0.67	0.5	0.5
microsculpture, disc:							
absent, 0							
5–20%, 0.33							
60%, 0.67							
100%, 1.0	1	0	0.33	0.67	0.16	1	0.67
absent, 0							
10–75%, 0.5							
100%, 1.0	2	0	0.5	1	0.25	1	0.5
pointed sculpture, disc:							
absent, 0							
3–5%, 1.0	1	0	0.5	0	0	1	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
		TAXA AND DISTRIBUTION OF CHARACTER STATES					
episternum,							
size basic setae:							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0	0.5
accessory setae:							
small, 0							
medium, 1.0	2	0	1	0	0	0	0
epimeron,							
size basic setae:							
very small, 0							
small, 0.5							
medium, 1.0	1–3	0	1	0.5	0.5	0.5	0.5
no. accessory setae:							
1, 0							
5–7, 1.0	2	0	1	0	0	0	0
sternite,							
no. accessory setae:							
2, 0							
10, 1.0	2	0	1	0	0	0	0
Mesonotum,							
size basic setae,							
PIM-I and PIE-A:							
medium, 0							
large, 1.0	1–3	1	1	1	1	0	0
PII–P							
absent, 0							
small, 0.5							
medium-small, 1.0	1–3	0	1	0.5	1	0.5	0.5

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
			TAXA AND DISTRIBUTION OF CHARACTER STATES				
no. accessory setae; disc:							
8, 0							
15–20, 0.33							
40, 0.67							
60–80, 1.0	2	0	1	0.33	0.33	0	0.5
epipleuron:							
1–2, 0							
4–5, 0.5							
7–13, 1.0	2	0	1	0	0.25	0	0.25
accessory setae size, posterior row:							
absent, 0							
small, 1.0	2	0	1	1	1	0.75	0.5
microsculpture, disc:							
10–50%, 0							
60–70%, 1.0	1	0	0	1	0	1	1
0–5%, 0							
20–40%, 0.5							
90–100%, 1.0	2	0	0.5	1	0.5	1	1
pointed sculpture, disc laterally:							
5–15%, 0							
25–35%, 1.0	1	0	0	0	0	1	0.5
anterior band,							
absent, 0							
30–50%, 0.5							
100%, 1.0	2	0	0.25	0	0	0.5	1
posterior band							
absent, 0							
30–50%, 0.5							
100%, 1.0	1–3	0	0	0	0.25	0.5	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
		TAXA AND DISTRIBUTION OF CHARACTER STATES					
anterior pleurite,							
basic seta size:							
very small, 0							
medium, 1.0	2	0	1	0	0	0	0
epipleuron,							
basic seta size:							
small, 0							
medium, 0.5							
very large, 1.0	1	0.5	1	0.5	0.5	0	0.5
medium-small, 0							
large, 1.0	2–3	0	1	0	0.5	0	0
no. accessory setae:							
1–3, 0							
9–16, 1.0	2	0	1	0	0.5	0	0
accessory setae size:							
absent, 0							
very small, 0.5							
medium-small, 1.0	2–3	0	1	0.5	0.5	0.5	0.5
microsculpture:							
absent, 0							
single-pointed, 1.0	2–3	0	0	0	0	0	1
episternum,							
no. accessory setae:							
1, 0							
3–6, 1.0	2	0	1	0	0	0	0
epimeron,							
no. accessory setae:							
1, 0							
4–10, 1.0	2	0	1	0.5	0	0	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
anterior sternite,							
basic setae size:							
absent, 0							
very small, 1.0	1	0	1	1	1	1	1
absent, 0							
small, 0.5							
medium, 1.0	2–3	0	1	0.5	0.5	0.5	0.5
no. accessory setae:							
0, 0							
2–3, 1.0	2	0	1	0	0	0	0
sternite,							
basic setae size:							
small, 0							
medium, 1.0	1	0	1	1	1	0	1
medium, 1.0	2	0	1	0	0	0	0
no. accessory setae:							
0, 0							
3, 1.0	2	0	1	0	0	0	0
Abdomen, terga,							
basic setae size,							
AII and AIM (1–8):							
medium, 0							
large, 1.0	1	0	1	0	0	0	0
small, 0							
medium, 1.0	2–3	0	1	1	1	1	1
AIM (1–8):							
similar on all, 0							
abruptly smaller, 1.0	1–3	0	0	0	0	1	0

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
			TAXA AND DISTRIBUTION OF CHARACTER STATES				
PII-P (1–8):							
very small, 0							
small, 0.5							
medium, 1.0	1–3	0	1	0	0	0	0.5
MPP-E (9):							
absent, 0							
small, 1.0	2–3	0	1	1	0.5	0.5	1
AM–P (10):							
very small, 0							
small, 0.5							
large, 1.0	1	0.5	1	0.5	0.5	0	0.5
small, 0							
medium, 0.5							
large, 1.0	2–3	0	1	0.5	0.75	0.5	0.5
PI–P (10):							
small, 0							
medium, 0.5							
large, 1.0	2–3	0	1	0.5	1	0.5	0.5
no. accessory setae, disc (1–8):							
7–10, 0							
15–20, 0.33							
25–30, 0.67							
40, 1.0	2	0	1	0.33	0.5	0	0.5
urogomphus (9):							
7, 0							
15–25, 1.0	2	0	1	0	0.5	0	0
disc (10):							
absent, 0							
2–3 major, 1.0	2	0	1	0	0.5	0	0

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Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
			TAXA AND DISTRIBUTION OF CHARACTER STATES				
absent, 0 1 minor, 0.1 4–5 minor, 0.2 20 minor, 1.0	2	0.2	1	0.1	0.15	0	0.05
position, acc. setae, antero-lateral major: lateral, 0 antero-dorsal, 1.0	2–3	0	0	0	0	1	1
microsculpture, type, anterior 0.5, disc: single-pointed, 0 multi-pointed, 1.0	1	1	0	1	1	1	1
disc (2–4): absent, 0 single–pointed, 0.5 multi-pointed, 1.0	2–3	0	0.25	0	0.5	0.5	1
urogomphus (9): scale-like, 0 single-pointed, 1.0	2–3	0	1	0	1	0	0
pointed sculpture, disc (4–5): 5%, 0 100%, 1.0	2	0	1	1	0.5	1	1
terga no., restricted: 1–3, 0 1–7, 1.0	2	1	0	0	0.5	0	0
anterior band (1–8): 0–5%, 0 100%, 1.0	1	0	0	0	0	0	1

(continued on next page)

Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
0%, 0							
50%, 0.5							
100%, 1.0	2	0	0.5	0	0	1	1
anterior band (9):							
0%, 0							
10%, 0.5							
100%, 1.0	2	0	0.5	0	0.25	1	1
epipleuron, shape (1–8):							
entire, 0							
divided, 1.0	2–3	0	1	0	0	0	0
basic seta size, anterior seta:							
medium, 0							
large, 1.0	1–3	0	1	0	0	0	0
anterior seta (1–8):							
similar on all, 0							
abruptly changed, 1.0	1–3	1	0	1	1	1	1
anterior seta (9):							
small, 0							
medium, 1.0	1–3	0	1	0	1	0	0.5
no. accessory setae:							
3–4, 0							
8, 0.33							
12–15, 0.67							
30, 1.0	2	0	0.67	0.33	0.67	0.33	0.5
hypopleuron, (1–8): no. accessory setae:							
4–6, 0							
12–16, 0.5							
20, 1.0	2	0	1	0	0.5	0	0.75

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Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	D	B	A	N	E	Et
			TAXA AND DISTRIBUTION OF CHARACTER STATES				
accessory setae size, major setae:							
medium, 0							
large, 1.0	2	0	0	1	1	1	1
minor setae:							
very small, 0							
small, 0.5							
medium, 1.0	2	0	1	0.5	1	0.5	0.5
sternite, no. accessory setae (1):							
2–6, 0							
8–16, 1.0	2	0	1	0	0	0	0
(2–7):							
8–20, 0							
30–40, 1.0	2	0	1	0	0	0	0
(8):							
8–15, 0							
20–25, 0.5							
40–45, 1.0	2	0	1	0	0.25	0	0
(9):							
absent, 0							
4–6, 0.5							
16–26, 1.0	2	0	1	0	0	0	0.5
(10), major setae:							
2, 0							
3, 0.5							
5, 1.0	2	0	1	0.5	0.5	0	0
(10), minor setae:							
3–4, 0							
6, 0.5							
14, 1.0	2	0.5	1	0	0.25	0	0.5

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Table 49 (continued)

CHARACTER AND CHARACTER STATES	Stage	TAXA AND DISTRIBUTION OF CHARACTER STATES D	B	A	N	E	Et
microsculpture: absent, 0 15% of (9), 0.5 30% of (9), 1.0	1	0	1	1	0.5	1	1
(2–9): single-pointed, 0 s. and m. pointed, 0.5 multi-pointed, 1.0	2–3	0.5	0.5	1	1	0	0
external poststernite, no. accessory setae, (1): 1, 0 2–4, 0.5 7, 1.0	2	0	1	0.5	0.5	0.5	0.5
(2–7): 3–4, 0 7–10, 1.0	2	0	1	0	0.5	0	0
internal poststernite, basic int. seta size, (1–8): very small, 0 small, 0.5 medium-small, 1.0	1–3	0	1	0	0	0	0.5
(9): very small, 0 small, 0.5 medium-small, 1.0	1–3	0	1	0	0	0	0.5
no. accessory setae, (1): 0–2, 0 6, 1.0	2	0	1	0	0	0	0

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Table 49 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES					
	Stage	D	B	A	N	E	Et
(2–7):							
1–2, 0							
3–4, 1.0	2	0	1	0	0.5	0	0

Table 50. Distribution of selected characters of adults among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES					
		D	B	A	N	E	Et
Clypeus, *setae:*							
2, a							
4, A	2	a	a	a	a	A	a
Eye, *convexity:*							
typical, b							
very prominent, B	2	b	b	B	B	B	B
Cornea, *thickness:*							
thinner ant., c							
similar, C	2	c	c	c	c	C	C
Frons, *lateral sulci:*							
straight, d							
octagonal, D	3	d	D	d	d	d	d
Mentum, *no. setae:*							
2, e							
4, E	2	e	E	e	e	e	e
Submentum, *no. setae:*							
8, f							
6, F	2	f	f	f	f	f	F
Pronotum, *lat. setae:*							
2, g							
1 or 0, G	1	g	g	G	G	G	G
lat. margin:							
narrow, h							
explanate, H	2	h	H	h	h	h	h
no. disc impr.:							
absent, i							
1 or more, I	3	i	i	I	I	I	I

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES					
		D	B	A	N	E	Et
post fringe:							
ended bef. hind angle, j							
ended at hind angle, J	2	j	j	j	j	J	J
shape fringe setae:							
narrow, scimitar, k							
wide, scimitar, K	1	k	k	k	k	K	K
Epist.: *epim. suture:*							
distinct, l							
indistinct, L	1	l	l	l	l	L	L
Prosternum, *lat. marg.:*							
sinuate, m							
angulate, M	1	m	m	m	M	m	m
ant. fringe:							
1 type setae, n							
2 types setae, N	1	N	n	n	n	n	n
discal setae:							
present, O	2						
absent, O– and o	1	o	o	O	O–	O	O–
Scutellum, *b. ridge:*							
absent, p							
present, P	2	p	P	p	p	p	p
Mesosternum, *coxal setae:*							
absent, q or Q–	1						
present, Q	2	q	q	q	q	Q	Q,Q–
lat. ridge:							
absent, r or R–	1						
present, R	2	r	R	R	R–,R	R–	R–

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	D	TAXA AND DISTRIBUTION OF CHARACTER STATES B	A	N	E	Et
Metasternum, *antero-medial setae:*							
absent, s							
present, S	2	s	s	S	S	S	S
lat. setae:							
present, T	2						
absent, t and T–	1	t	t	T	T–	T	T,T–
Abdominal sterna 3-4 *accessory setae:*							
absent, u or U–	1						
present in males, U	2						
on m. and f., U′	3	u	U,U–	U′	U′	U′	U′
Elytra *setigerous punct.:*							
15–20 microns, V							
30 microns, V	2						
40–50 microns, V′	2	v	V′	V	V′	V′	V′
striae, disc:							
present, w							
7–8 irregular, W1	2						
absent, W2	3	w	W1	W2	W2	W2	W2
striae 2 and 3:							
entire, x							
catenate ant. and post. to setigerous puncture, X	3						
catenate ant. to setigerous punct., X1	1						
circle around set. punct. larger X2	3	x	X,X1	X2	X2	X2	X2

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES					
		D	B	A	N	E	Et
interval, no. rows setigerous punct.:							
3, y							
3, 5 and 7, Y	2						
3, 5, Y–	1	y	Y–	Y	Y	Y	Y
intervals, 4, 6 and 8:							
entire, z							
catenate, Z	2						
cat. mirror-like, Z1,Z2	3	z	Z–Z1	Z2	Z2	Z2	Z2
Foreleg, *trochanter:*							
1 seta, AA1	1						
2 setea, aa							
3 setae, AA2	2	aa	AA1	aa	aa	AA2	aa
tibia, post. fringe:							
4–8 setae, ab							
0 or 1 seta, AB	1	ab	ab	ab	AB	AB	AB
no. setae postero-medial row m. vs. f.:							
similar, ac							
very dissimilar, AC	2	ac	ac	ac	AC	AC	AC
no. enlarged male tarsomeres:							
4, ad							
3, AD	1	ad	ad	ad	ad	AD	AD
Midleg, *coxa no. setae:*							
1 or 2, ae							
numerous, AE	2	ae	ae	AE	AE	AE	AE
trochanter no. setae:							
0, AF1	1						
1 or 2, af							
3, AF2	2	af	af–AF1	af	af	AF2	af

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES					
		D	B	A	N	E	Et
tibia, male apico-internal point:							
absent, ag or AG–	1						
present, AG	2						
AG*=AG,AG–		ag	AG*	AG	AG*	AG	AG*
Hind leg, *coxa extension, setae:*							
absent, ah							
inner 0.5, AH	2						
on all, AH′	1	ah	ah,AH	AH	AH	AH′	AH
femur, no. setae:							
5 or less, ai							
20 or more, AI	2						
6 or 12, AI–	1	ai	ai	AI	AI–	AI	AI
Microsculpture, *dorsum:*							
alveolae flat to subconvex, aj							
alveolae convex, AJ	1	aj	aj	AJ	aj	aj	aj
Male genitalia, *median lobe, baso-dorsal surface:*							
closed, ak							
open, AK	3	ak	AK	AK	AK	AK	AK
med. lobe, stylet post.:							
narrow, al							
enlarged, AL	3	al	AL	AL	AL	AL	AL
dorsum, right apex:							
smooth, am							
lat. point, AM	2	am	am	AM	am	am	am

(continued on next page)

Table 50 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES					
		D	B	A	N	E	Et
parameres, seta size:							
short, an							
long, AN	1	an	an	an	an	an,AN	an–AN
Ovipositor, *stylus, apical sclerite setae:*							
2 small, ao							
2 very small, AO	1						
1 very small, AO′	1						
0, AO″	1	ao	ao	ao	AO′	AO″	AO″

Table 51. Distribution of selected characters of larvae among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES					
Stage	Weight	D	B	A	N	E	Et
Head, *color:*							
yellow and brown, a							
orange, A	1–3	1	a	a	A	a	a	a
Nasale							
med. projection:							
short, b							
long, B		2					
very long, B′		2					
extr. long, B"	1–3	1	b	B	B′	B′	B"	B"
projection, apex:							
single-pointed, c							
3–pointed, C	1–2	2	C	c	c	c	c	c
teeth, position:							
lateral, d							
medial, D	1–2	1	d	D	d	d	d	d
teeth size:							
small, e or E3		1					
very small to absent E1		1					
large, E2	2	1	e	E2	E2	E2,E1	E1	E3
Parietale							
occipital suture:							
1.0–1.2 scape length, f							
0.2–0.6 scape length, F	2–3	1	f	f	f	f	F	F

(continued on next page)

Table 51 (continued)

CHARACTER AND CHARACTER STATES		TAXA AND DISTRIBUTION OF CHARACTER STATES						
Stage	Weight	D	B	A	N	E	Et	
length:								
long head, g								
short head, G	1–3	1	G	g	g	g	G	G
pore VEP–A, position:								
int. to VEP–P, h								
ext. to VEP–P, H	1–3	1	h	h	H	H	H	H
Mandible, *base width:*								
narrow, i								
wide, I	1–3	2	i	i	I	I	I	I
Stipes, *ext. surface:*								
sclerotized, J2								
narrow unscl. band, j								
unscl. band + bump, J1	2–3	3	j	J2	j	J2	JI	JI
int. brush, no. rows:								
1 apical 0.33, k								
2–3, K	1–3	1	k	k	k	k	K	K
acc. setae, external surface:								
absent, l								
present, L	2–3	2	l	L	l	l	l	l
Galeomere 1, *seta:*								
virtually absent, m								
v. small M	1–3	1	m	M	M	M	M	M
Lacinia, *shape:*								
coniform, n								
suggested, N	1–3	1	n	n	N	N	N	N

(continued on next page)

Table 51 (continued)

CHARACTER AND CHARACTER STATES			TAXA AND DISTRIBUTION OF CHARACTER STATES					
Stage	Weight	D	B	A	N	E	Et	
seta size:								
small, o								
extra. small,O	1–3	1	o,O	O	o	o	o	o
Pronotum, *disc,*								
accessory setae:								
4–5, p								
10–20, P		1						
30–40, P1		1						
90 or more, P2	2	1	p	P2	P	P	P	P1
Pronotal epipleuron								
accessory setae:								
O, q								
2–3, Q		1						
5–7, Q1		1						
12–14, Q2	2	1	q	Q2	Q	Q,Q1	Q	Q
Mesonotum, *disc,*								
no. acc. setae:								
8–10, r or R4		1						
12–15, R1		1						
20–40, R2		1						
60–70, R3	2	1–2	r	R3	R4	R1	R4	R2
Abdomen, *terga 1–8*								
seta AIM size:								
similar on 1–8, s								
abruptly smaller, S	1–2	2	s	s	s	s	S	s
epipleuron, size								
anterior seta:								
small, t								
medium–small, T	1–3	1	t	t	t	T	t	t

(continued on next page)

Table 51 (continued)

CHARACTER AND CHARACTER STATES			TAXA AND DISTRIBUTION OF CHARACTER STATES					
Stage	Weight	D	B	A	N	E	Et	
sternites 2–7,								
no. acc. setae:								
14–25, u								
30–40, U1		1						
90–150, U2	3	1	u	U2	u	u	u	U1
internal								
poststernite,								
int. seta size 1–8:								
very small, v								
small, V	1–3	1	v	V	v	v	v	V
microsculpture,								
extension, nota:								
restricted or absent, w								
widespread, W	1–3	1	w	w	W	w	W	W
pointed sculpture,								
terga 4–5:								
on all of disc, x								
5% of disc, X	2	1	X	x	x	x,X	x	x
urogomphus:								
single-pointed, y								
scale–like, Y		2						
absent, Y′	1–3	1	y	Y	Y′	y,Y′	y	y
sternite 9:								
no meshes, z								
meshes distinct, Z	3	2	z	z	Z	z	z	z

Table 52. Distribution of selected characters of adults among groups of subgenus *Neoelaphrus* and evolutionary classication of the character states. (Taxa abbreviated 'u' for *uliginosus*, 'f' for *fuliginosus* and 'c' for *cupreus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	u	f	c
Eye, *cornea thickness:*				
40–60 Microns, a				
100 microns, A	1	a	A	a
Pronotum, *lateral bead:*				
thick, 20–30 microns, b				
thin, 10–15 microns, B1	1			
absent, B2	1	b	b,B2	B1
lateral margin, lat. view:				
straight, c				
sinuate at middle, C	2	C	c	c
termination of post. fringe:				
40–120 microns from hind angle, d				
150–200 microns, D	1			
200–250 microns, D′	1	d	D,D′	D′
disc, antero-submedial impr.:				
absent, e				
present, E	1	E,e	e	e
Abdomen, *sterna 5 and 6 accessory setae:*				
present, f				
absent, F or F–	1	f	F	f,F–
Foreleg, *males, base post. spur:*				
withour large point, g				
with large point, G	1	g	G	g
Punctures, *surrounding surface of pleura:*				
narrowly or not depressed, h				
widely depressed (80 microns), H	2	h	H	h

(continued on next page)

Table 52 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	u	f	c
size, pleura:				
30–45 microns, i				
20–30 microns, I	1	i	i	I
Male genitalia, *apex median lobe*				
lateral view:				
narrow, j				
wide, J1	1			
very wide, J2	1	j	J1	J2,j

Table 53. Distribution of selected characters of adults among species of *uliginosus* group and evolutionary classification of the character states. (Taxa abbreviated 's' for *splendidus*, 'J' for *japonicus*, 'u' for *uliginosus*, 'p' for *pyrenaeus*.)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES s	j	u	P
Dorsum, *color:*					
Green, k					
brilliant green, K	1				
brown copper, K1	1	K	K1	k	K1
Color of elytral pits:					
purple metallic, l					
green metallic, L	1	L	l	l	l
Pronotum, *antero-lateral impr.:*					
absent, m					
present, M	1	m	M	M	M
Elytra, *sutural mirrors:*					
flat and distinct, n					
convex and distinct, N1					
flat and indistinct, N2	1	N1	n	n	N2
no. rows mirrors:					
2, o					
4, O	1	O	o	o	o
Hind leg, *coxa, no. setae:*					
3–7, p					
8–15, P	1	P	p	p	p
Punctures, *density pronotum:elytra:*					
similar, q					
dissimilar, Q	2	Q	q	q	q
intervals 4, 6 and 8					
30–40 microns apart, r					
100–150 microns apart, R1	1	r	R1	r	r

(continued on next page)

Table 53 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES s	j	u	P
Miscrosculpture meshes:					
widespread, s					
very restricted, S	1	S	s	s	S
Male genitalia,					
apex median lobe,					
dorsal view:					
narrow + straight					
(20–30 microns), t					
wide + twisted					
(60–65 microns), T1	1	t	t	T1	T1
lateral view:					
narrows, j					
enlarged ventrally, J3	1	j	J3	j	j

Table 54. Distribution of selected characters of adults among species of the *fuliginosus* group and evolutionary classification of the character states. (Taxa abbreviated 'f' for *fuliginosus*, 'l' for *lindrothi*, 'c' for *cicatricosus*.)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Weight	f	l	c
Color, *dorsal:*				
green, k				
very dark copper, K2	1			
silvery-brass, K3	1	k	K3	K2
Color, *tarsomeres:*				
purple, u				
green, U	1	U	u	u
Pronotum, *lateral bead:*				
thick (20–30 microns), b				
absent, B2	1	b	B2	B2
termination of post. fringe:				
150–200 microns to hind angle, D				
200–250 microns to hind angle, D′	1	D	D′	D′
Abdomen, *sternum 7, males, accessory setae:*				
present, v				
absent, V	1	v	V	V
Elytra, *sutural mirrors:*				
distinct and flat, n				
indistinct and flat, N2	1	n	N2	n
Foreleg, *trochanter, setae:*				
2, w				
1, W	1	w	w	W
Punctures, *density, intervals 4, 6 and 8:*				
30–40 microns, r				
10–200 microns, R2	1			
10–30 microns, R3	1	r	R3	R2

Table 55. Distribution of selected characters of adults among species of the *cupreus* group and evolutionary classification of the character states. (Taxa abbreviated as 's' for *sibiricus*, 'cu' for *cupreus*, 'cl' for *clairvillei*, 'o' for *olivaceus*, and 'l' for *laevigatus*.)

CHARACTERS AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES				
		s	cu	cl	o	l
Color, *dorsum:*						
green, k						
dark copper, K4						
black, K5	1	k	K4	k	k	K5
Pronotum, *discal impr.:*						
2, x						
1, X	1	x	x	X	x	X
Prosternum, *intercoxal process:*						
with setae, y						
without setae, Y	1	y	y	y	Y	Y
Abdomen, *sterna 5 and 6:*						
with accessory setae, f						
without, F–	1	f	f	f	F–	f
Abdomen, *sternum 7, males:*						
with accessory setae, v						
without, V	1	v	v	v	V	v
Elytra, *mirrors:*						
distinct, n						
indistinct, N2	1	n	n	N2	N2	N2
pits, lateral ridges:						
separated, z						
fused, Z	1	z	z	Z	Z	Z
setigerous punctures:						
distinct, aa						
indistinct, AA	1	aa	aa	aa	aa	AA
Midleg, *tibia,*						
apico–internal points:						
present, ab						
absent, AB	1	ab	ab	ab	AB	AB

(continued on next page)

Table 55 (continued)

CHARACTERS AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES s	cu	cl	o	l
Punctures, *size, dorsum:*						
20–30 microns, ac						
10–20 microns, AC	1	ac	ac	ac	AC	AC
density, pleuron:						
30–40 microns apart, ad						
10–20 microns apart, AD	1	ad	ad	ad	AD	AD
density, intervals 4, 6 and 8:						
30–40 microns apart, r						
10–20 microns apart, R4	1					
10–200 microns apart, R5	1					
200 microns or more, R6	1					
50–100 microns apart, R7	1	r	R7	R5	R4	R6
density, metasternum, antero-medially:						
50–100 microns apart, ae						
20 microns apart, AE	1	ae	ae	ae	AE	ae
no. in pits:						
8–15, af						
3–5, AF	1	af	af	af	af	AF
Microsculpture meshes, *dorsum:*						
expanded, s						
very restricted, S	2	s	s	S	S	S
Male genitalia, *apex med. lobe, dorsal view:*						
thin and straight (20–30 microns), t						
thick (50 microns) + twisted, T2	1	t	t	T2	t	t

(continued on next page)

Table 55 (continued)

CHARACTERS AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES				
		s	cu	cl	o	l
length of apex in dorsal view:						
moderate, ag						
long. AG1	2					
short, AG2	2	AG1	AG1	ag	AG2	AG2
lateral view:						
narrow, j						
wide, J2	1	J2	J2	j	j	j

Table 56. Distribution of selected characters of larvae among species of subgenus *Neoelaphrus* and evolutionary classification of the character states and their weight (taxa abbreviated: 'fu'=*fuliginosus*, 'li'=*lindrothi*, 'ci'=*cicatricosus*, 'cu'=*cupreus*, 'cl'=*clairvillei*, 'ol'=*olivaceus*, 'la'=*laevigatus*).

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
Nasale;									
toothed, ah									
smooth,AH	1–3	1	ah	AH	AH	ah	ah	ah	ah
Parietale, *color:*									
75% dark, ai									
10–20% dark, AI	2–3	1	AI	AI	AI	ai	ai	ai	ai
Epicranial suture:									
long, aj									
short, AJ	1–3	1	AJ	AJ	AJ	aj	aj	aj	aj
microsculpture dorsal extension:									
15–25%, ak									
5–10%, AK1		1							
0–1%, AK2		1							
50–80%, AK3	1	1	AK1	AK1	AK2	ak	ak	AK3	AK3

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
Pronotum, *no. acc. setae:*									
25–30, al									
70–90, AL1		1							
90–120, AL2	3	1	AL1	AL2	AL2	al	al	al	al
Metanotum, *pointed sculpture, near suture:*									
present and narrow, am									
absent, AM1		1							
present and wide, AM2	2–3	1	AM1	am	AM1	am	am	am	AM2
pointed sculpture, lateral:									
present, an									
absent, AN	2–3	1	an	an	AN	an	an	AN	AN
no. acc. setae:									
15–25, ao									
35–45, AO	3	1	ao	AO	AO	ao	ao	ao	ao

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
epipleuron, no. acc. setae:									
0–3, ap									
5–10, AP	2–3	1	ap	ap	AP	ap	ap	ap	ap
Abdomen, *terga 1–8, no. acc. setae:*									
25–35, aq									
60–80, AQ1		1							
90–110, AQ2		1							
125–150 AQ3	3	1	AQ1	AQ2	AQ3	aq	aq	aq	aq
Urogomphus, *no. acc. setae:*									
7, ar									
9–14, AR		1							
20–40, AR′	2–3	1	AR	AR	AR′	ar	ar	ar	ar
terga 5–8, pointed sculpture:									
over, as									
restricted, AS	2–3	1	as	as	AS	as	as	as	as

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
anterior band of terga 1–8, pointed microsculpture:									
present, at									
absent, AT	2–3	1	at	AT	AT	at	at	at	at
anterior band of tergum 9, pointed microsculpture:									
present, au									
absent, AU	2–3	1	au	AU	AU	au	au	AU	AU
urogomphus, pointed microsculpture:									
present, av									
absent, AV	2–3	1	av,AV	av	AV	av	av	av	av
epipleura 2–7, no. acc. setae:									
15–20,aw									
25–35,AW1		1							
40–60, AW2	3	1	AW1	AW2	AW2	aw	aw	aw	aw

(continued on next page)

Table 56 (continued)

CHARACTER AND CHARACTER STATES	TAXA AND DISTRIBUTION OF CHARACTER STATES								
	Stage	Weight	fu	li	ci	cu	cl	ol	la
sternite 8, no. acc. setae:									
15–20, ax									
30–40, AX	3	1	AX	AX	AX	ax	ax	ax	ax
sternite 9, no. acc. setae:									
5–7, ay									
1–2, AY	3	1	ay	ay	ay	ay	ay	AY	AY

Table 57.Distribution of selected characters of adults among species of subgenus *Elaphrus* and evolutionary classification of the character states and their weight (taxa abbreviated: 'ma'=*marginicollis*, 'lh'= *lheritieri*, 'mi'=*mimus*, 'vi'=*viridis*, 'hy'=*hypocrita*, 'ru'=*ruscarius*, 'le'=*lecontei*, 'ca'=*californicus*, 'fi'=*finitimus*, 'am'=*americanus* 'tu'=*tuberculatus*, 'ri'=*riparius*, 'co'=*comatus*, 'pa'=*parviceps*, 'ti'=*tibetanus*).

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES														
		ma	lh	mi	vi	hy	ru	le	ca	fi	am	tu	ri	co	pa	ti
Pronotum, *no. acc. setae:*																
absent, a																
on head and pronotum, A1	2															
on pronotum only, A2	2	a	A2	A1	A1	a	a	a	a	(A1–2)	(A1–2)	(A2)	(A2)	a	A2	A2
lateral margin, sinuation:																
beaded, b																
not beaded, B	1	b	B	B	B	B	B	B	B	B	B	B	B	B	B	B
shape of margin:																
narrow, c																
explanate, C	2	c	C	C	C	c	c	c	c	c	c	c	c	c	c	c
punctures size:																
20–30 microns, d																
40–50 microns, D	2	D	d	d	d	d	d	d	d	d	d	d	d	d	d	d

(continued on next page)

Table 57 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES														
		ma	lh	mi	vi	hy	ru	le	ca	fi	am	tu	ri	co	pa	ti
punctures, pattern:																
sparcer laterally, e roughly equidistant, E	2	e	E	E	E	e	e	e	e	e	e	e	e	e	e	e
Prosternum, *puncture density:*																
20–40 microns apart, f 10–25 microns apart, F	1	f	f	f	f	f	f	F	F	F	F	f	f	f	f	f
Elytra, *main mirror, shape:*																
rectangular, g ovoid, G	1	g	G	G	G	g	g	g	g	g	g	g	g	g	g	g
pit size:																
moderate, h																
very large, H1	2															
absent, H2	2	h	H1	h	H2	h	h	h	h	h	h	h	h	h	h	h

(continued on next page)

Table 57 (continued)

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES														
		ma	lh	mi	vi	hy	ru	le	ca	fi	am	tu	ri	co	pa	ti
Abdomen,																
acc. set. distribution:																
not extended to edge, i																
extended to edge, I	1	i	i	i	I	i	i	i	i	i	i	I	I	I	I	I
acc. setae:																
similar in both sexes, j																
more in males, J	2	j	j	j	j	j	j	J	J	J	J	j	j	j	j	j
no. punctures on sternite 4																
40–60, k																
100–200, K1	1															
0–20, K2	1	k	k	k	k	k	k	K1	K1	K1	K1	k	k	k	K2	K2

Table 58. Distribution of selected characters of adults among species of subgenus *Elaphroterus* and evolutionary classification of character states and their weight (taxa abbreviated: 'pun'=*punctatus*, *'au'*=*aureus*, 'pur'=*purpurans*, 'an'=*angusticollis*, 'ul'=*ulrichi*).

CHARACTER AND CHARACTER STATES	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES pun	au	pur	an	ul
Pronotum, *lateral margin*						
well outlined medially, a						
suggested medially, A	1					
absent, A′	1	a	a	A′	A	A
postero–lateral puncture:						
present, b						
absent, B	1	b	b	b	b	B
Prosternal process, *acc. setae*						
4–6, c						
0–2, C	1					
0–, C′	1	c	C	C′	C′	C′
Metasternum, *posterior margin, acc. setae:*						
present, e						
absent, E	1	e	e	e	e	E
Elytral subsutural mirrors:						
similar width, f						
one or two narrower, F	3	f	F	F	F	F
Secondary sexual characters, *(on fore tarsi and mid-tibiae):*						
expressed normally, g						
absent, G1	3					
more characters expressed, G2	3	G1	g	G2	g	g
Mid-trochanter, *no. setae:*						
1, h						
2, H	2	H	h	h	h	h
Paramerers, *setae size:*						
long, i						
short I	1	i	i	I	I	I

Table 59. Distribution of selected characters of larvae among species of subgenus *Elaphroterus* and evolutionary classification of character states and their weight (taxa abbreviated:'au'=*aureus*, 'pur'= *purpurans*, 'an'=*angusticollis*, 'ul'=*ulrichi*).

CHARACTER AND CHARACTER STATES			TAXA AND DISTRIBUTION OF CHARACTER STATES			
	Stage	Weight	au	pur	an	ul
Parietale, *color:*						
mostly dark, j						
mostly pale, J	1–3	2	j	j	J	j
Nota and terga, *color:*						
dark brown, k						
with dark and pale parts,K	2–3	3	k	k	k	K
Mandible, *inner edge:*						
serrated, l						
smooth, L	1	1	l	L	L	L
Parietale, *sculpture dist.:*						
absent or almost, m						
10–25% dorsally, M						
50–80% dorsally, M′	1–3	1	m	M	M′	M′
epicranial suture:						
normal, n						
very short, N	1–3	1	N	n	n	n
Pronotum, *no. acc. setae:*						
25–35, o						
40–50, O		1				
55–65, O′	3	1	o	O	O′	O′
Mesonotum and metanotum, *no. acc. setae:*						
25–35, p						
45–55, P	3	1	p	p	P	P
Terga 1–8, *no acc. setae:*						
35–45, q						
40–60, Q	3	1	q	q	Q	Q

(continued on next page)

Table 59 (continued)

CHARACTER AND CHARACTER STATES	Stage	Weight	TAXA AND DISTRIBUTION OF CHARACTER STATES au	pur	an	ul
Epipleuron:						
narrow, r						
wide, R	3	2	r	r	r	R
Urogomphus, *no. very small acc. setae:*						
rare or absent, s						
numerous, S	2–3	2	s	s	S	S
knob development:						
small, t						
absent, T	2–3	2	t	t	t	T
Abdominal epipleura 2–7, *no. acc. setae:*						
about 20, u						
about 30, U		1				
about 40, U′	3	1	u	U	U′	U′

Table 60. Summation of steps used in determining character state polarities. A) Types of out-group evidence in determining a derived character state. B) Taxonomic category considered in out-group comparisons and their code. C) Type of out-group evidence used in determining a character state as derived for each character of listed tables. "*" denotes that a limited number of divergent taxa were examined.

A) TYPES OF OUT-GROUP EVIDENCE

Type	Definition
I	A Character state that is unique to a group within a considered category, assuming the character is not ancestral to that category – autapomorphy.
II	A unique character state appearing in considered taxa and its sister lineage – synapomorphy.
III	As I or II, but state exists in distantly related groups (on basis of other characters) within a considered category – autapomorphy or synapomorphy with evidence of convergent evolution.

B) CATEGORY CONSIDERED AND CODE

Tribe: (T); Genus: (G); Subgenus: (S); Species group: (E)

C) TYPE OF OUT-GROUP EVIDENCE FOR EACH CHARACTER IN EACH TABLE

(continued on next page)

Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
I (T)	C*, D, G, I, J, K, L, N, U, V, V′, X, Y–, AA1*, AA2*, AF1*, AF2*, AG, AL, AM, AO″	B′, C, I*, J1, L*, P2*, Q2*, R3*, S, U2*, Y	A*, G		G2, R
III (T)	A, B, E, G, H, S, T, U′, W1, W2, X1, X2, Y, Z, Z′, AE, AH, AH′, AI, AK, AN, AO, AO′	G, H, N, O, P, P1, Q, Q1, R1, R2, U1, W, X	B2		
I (G)	F, M, O, P, AB, AC, AD	A, D, F, K, Z,	C, D, D′, E, J2, W, AP, AR	B, C	B, G1, H, K, T
II (G)	Q, R, U	B, E2, J2, M			

(continued on next page)

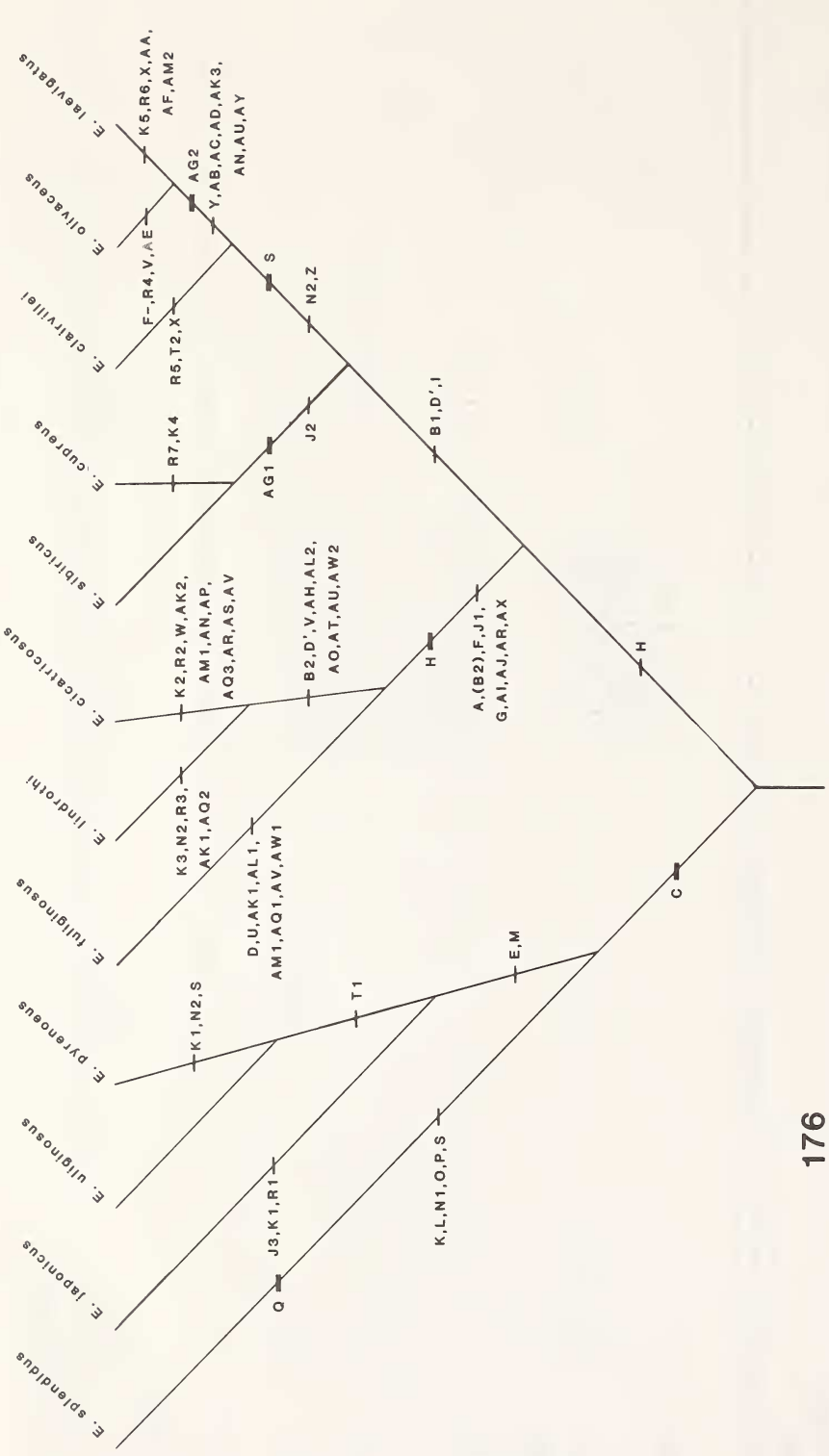
Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
III (G)	AJ	J2, R4, V, X, Y′	B1, H, K, L, Q, AB, AH, AL2, AQ2, AQ3, AR′	D, E	I
I (S)		T	J1, K3, O, R6, AA, AG1, AG2, AK2, AL1, AM2, AO, AQ1, AW1, AW2, AX	G, H1, H2, I, J, K1	A, E, S
II (S)	U–, AG–, AI–				F
III (S)	O–, Q–, R–, T–	E1, E3,	F–, K1, N1, N2, R5, R7, AI, AK3, AM1, AN, AT, AV	F, K2	A′, L, M′, O, O′, P, Q, U, U′

(continued on next page)

Table 60 (continued)

Tables OUT-group type	Table 50	Table 51	Tables 52 to 56	Table 57	Tables 58, 59
I (E)			I, J3, K5, P, R3, R5, X, Y, Z, AC, AD, AE, AF, AJ, AS, AY		J, M
II (E)			M		C, C′
III (E)			K2, K4, R1, R2, S, T1, T2, AK1, AU	A1, A2	



176

Fig. 176. Reconstructed phylogeny of species of subgenus *Neoelaphrus* based on adults and larvae. Capital letters refer to derived states of coded characters (see Tables 52 to 56). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

PHYLOGENY OF ELAPHRINI

Monophyly of Elaphrini

The tribe Elaphrini forms a monophyletic assemblage as shown by the following uniquely derived character states. Adults: presence of longitudinal keel-like microsculpture under the subapical portion of the elytron, and of lateral pairs of plates expanded apically into a curved row of points on abdominal tergum 7 (see figures 4 to 7 in Bauer, 1973). These two structures appear functionally related (Lindroth, 1954; Bauer, 1973, 1976), but are apparently not sound-producing organs (Forsythe, 1978). Larvae: the urogomphus of the second and third instar larvae, (except that of *E. ulrichi*) with unusual pattern of large and small projections (Figs. 93 to 103).

The elaphrine sister group

The Elaphrini are not clearly positioned in the general system of the Carabidae, as shown by the following points of view. Jeannel (1941, 1942) discussed relationships of the elaphrines to other carabid tribes. He put them near Migadopini, a tribe of the southern hemisphere. Among his "Caraboidea Simplicia", adults of Migadopini and of Elaphrini share similar setose parameres, probably an ancestral state shared with various older lineages of carabids and other adephagous beetles, and with lineages of similar age (Broscini, Patrobini, Nomiini, Melaenini and Scaritini). However, elaphrine adults have narrow metepimera, a feature which locates the tribe near Jeannel's "Caraboidea Limbata, Scrobifera or Stylifera". Therefore, Elaphrini are probably not related to Migadopini.

Bell (1967) put the Elaphrini in the Isopleuri with Loricerini, Scaritini and Cicindelini. However, the Isopleuri are not defined by any shared derived character state. Ball's (1956) study of broscine male genitalia gave the best evidence about relationships of Elaphrini with Stylifera. The complex posterior sclerites x and y seen in Broscina (Figs. 36a, b) seem homologous with the elaphrine stylet and anterior cup-shaped sclerite. Sclerite x of the Broscina is made of two long dorsal adjacent sclerites and is membranous ventrally; the ejaculatory duct penetrates the posterior end. This stylet is also found in males of Melaenini, (Figs. 37a, b) a little known tribe. In Melaenini, the sclerite x is similar to that of *Diacheila*. Moreover, in adults of Melaenini, some Broscini and Elaphrini (except those of *Diacheila*), the antero-medial portion of setigerous punctures of elytron is elevated and cone-like. Adults of Melaenini and Elaphrini also have an oblique comb dorso-apically on the midtibia, but lack a dorsal brush on the midtibia (Erwin, 1978). However,adults of Elaphrini differ from those of the Broscina and Melaenini in having disjunct middle coxae and narrow metepimera.

Sclerites x and y are probably uniquely derived states. Thus, the Elaphrini, Melaenini and the Broscina should be considered related. Because I have only this evidence. I cannot say if this state was lost or did not evolve in the remaining Broscini and other tribes with setose parameres, and if a long stylet-like sclerite x is derived relative to the shorter sclerite in males of Broscina.

In the general frame of carabid classification, the Elaphrini and its related groups, the Melaenini and the Broscina, are related to the Nomiini, Patrobini and remaining subtribes of Broscini. They share with most members of these tribes a posterior transverse impression behind the eyes (probably a derived state). Elaphrini may be the earliest lineage among these tribes. In adults of these tribes, the middle coxae are conjunct (a derived state).

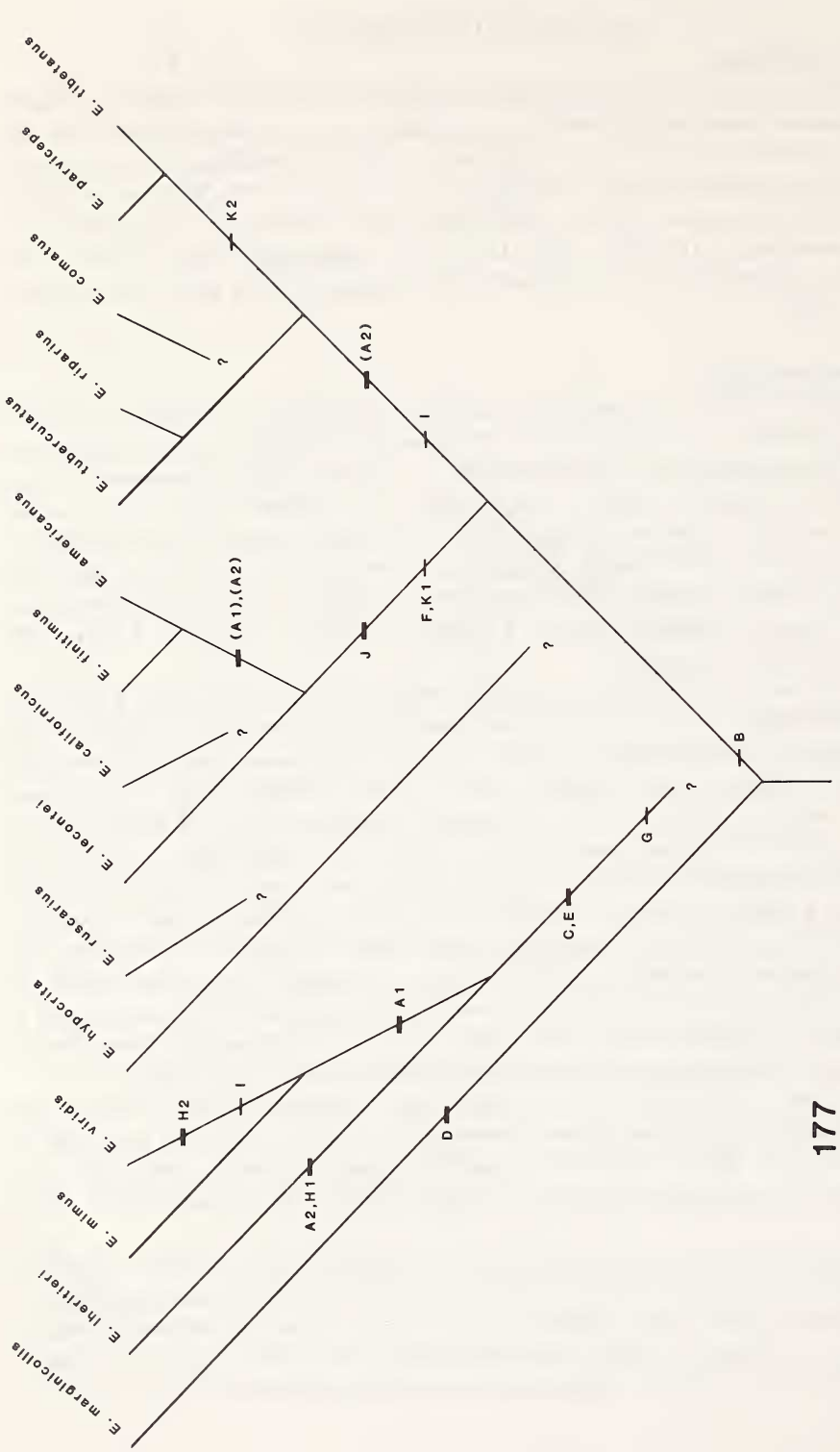


Fig. 177. Reconstructed phylogeny of species of subgenus *Elaphrus* based on adults. Capital letters refer to derived states of coded characters (see Table 57). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines, high.

Relationships among genera and subgenera of Elaphrini

Adults.— The following derived character states show that species of *Blethisa* and *Elaphrus* have a common ancestor, exclusive of *Diacheila*: median lobe of males sharply divided into thickly (ventral and basal surface) and thinly (lateral and dorsal surfaces) sclerotized portions; stylet of internal sac extended anterad to base of ejaculatory duct for muscle attachment; setigerous punctures of interval 3, 5 and 9 cordiform, when completely outlined, and elevated in anterior portion of emargination. *Diacheila* is the sister group of the above genera.

Each genus is monophyletic as shown by uniquely evolved character states (see Fig. 175a for details). The ancestors of *Diacheila* evolved narrow and scimitar-shaped setae on the anterior margin of the prosternum; those of *Blethisa* evolved 8-shaped frontal grooves; and those of *Elaphrus* evolved elytral pits and mirrors, and ominent eyes.

The species of *Elaphrus* were grouped by Semenov (1926) into five subenera of which four are retained here. The naturalness of each subgenus is clearly suggested by character states indicated in Fig. 175a. The main evidence for relationships between subgenera of *Elaphrus* is based on reduction of apical setae on apical sclerites of the stylus of the ovipositor. Females of *Arctelaphrus* have two very small setae, those of the ancestor of *Neoelaphrus* lost one, and those of *Elaphroterus* and *Elaphrus* lost both (for details see Fig. 175a).

Larvae.— Synapomorphies confirm most groups of adults, but they are few and of low weight (for details see Fig. 175b).

A close relationship of *Blethisa* and *Elaphrus* is suggested by the following shared derived states: increased number of accessory setae on all sclerites of the second and third instar larvae and larger seta on galeomere 1. In these two characters, larvae of *Diacheila* are more similar to members of other tribes. The naturalness of each genus was demonstrated by uniquely derived character states indicated in Fig. 175b.

The common ancestor of *Elaphrus* and *Elaphroterus* evolved a shorter head, shorter epicranial suture, and two or more rows of setae in the apical 0.3 of the inner dorsal surface of the stipes. However, I failed to show if *Neoelaphrus* is ancestral to all subgenera, shares a recent ancestor with *Arctelaphrus* or with the remaining subgenera.

Relationships among species of subgenus *Neoelaphrus*

Adults.— The species of *Neoelaphrus* are arranged in three groups. The naturalness of each group is suggested by the following shared derived character states (see Fig. 176 for details). Adults of the ancestor of the *uliginosus* group gained four to six impressions on each side of the pronotal disc, and the prontal lateral margin in lateral view became sinuate near the middle; those of the *fuliginosus* group gained a cuticular projection at the base of the anterior and posterior spurs of the male foretibia, and evolved a thick (100 microns) eye cornea; those of the *cupreus* group evolved a narrower (10 to 15 microns) bead on the lateral margin of the pronotum.

The main evidence for the relationships between these three groups is area of termination of the fringe of the pronotal posterior margin. In members of *Diacheila* and *Arctelaphrus* the fringe is terminated behind the postero-lateral impression (30 to 120 microns from hind angle). Thus, the *fuliginosus* and *cupreus* groups are sister groups since they share the following derived state: fringe of posterior margin of pronotum ended before postero-lateral impression (200 to 250 microns from hind angle).

The *uliginosus* group has four and probably five known species. *E. uliginosus* and *E. pyrenoeus* are sister species as suggested by the thick and twisted apex of the male median lobe in dorsal view. *E. japonicus* is closely related to the *E. uliginosus* - *E. pyrenoeus* lineage as shown by the major development of impressions on the pronotum.

The *fuliginosus* group has three extant species. Of these, *E. lindrothi* and *E. cicatricosus* share the following derived characters: loss of the bead on the lateral margin of pronotum, and of accessory setae on abdominal sterna 5, 6 and 7 of both sexes.

The *cupreus* group has five extant species, which are arranged in two subgroups. Adults of the ancestor of the *sibiricus* subgroup evolved a very elongate and wide (in lateral view) apex of the male median lobe. Those of the *clairvillei* subgroup gained a brilliant dorsal surface (lack of microsculpture, or presence of meshes under smooth transparent layer), and the lateral ridges of the elytral pits became fused. In the *sibiricus* subgroup, two species are known: *E. cupreus* and *E. sibiricus*. The *clairvillei* subgroup has three species. Of these, adults of *E. olivaceus* and *E. laevigatus* evolved dense pleural punctation, a short apex of the median lobe, and fine dorsal punctures, and lost the cuticular projection at the base of inner spur on male midtibia.

Larvae.— Two groups were studied: the *fuliginosus* and *cupreus* groups (Fig. 176). Naturalness of the *fuliginosus* group is shown by an unusual abundance of accessory setae on many sclerites, by reduction of sculpture on parietale, by a shorter epicranial suture, and by a much paler parietale. I failed to find shared derived character states between members of the *cupreus* group. Among the three species of the *fulliginosus* group, *E. lindrothi* and *E. cicatricosus* share the following derived character states: abundant accessory setae on many sclerites, reduced pointed microsculpture on anterior bands of terga, and loss of teeth on nasale. Less can be said about relationships between species of the *cupreus* group, except that adults of *E. olivaceus* and *E. laevigatus* share the following derived character states: marked development of microsculpture on the parietale of the first instar larvae, lack of microsculpture on the pronotum laterally and on the anterior band of tergum 9, and reduction of accessory setae on the sternite 8.

Reconstructed phylogeny based on adults and larvae, when shown, is fully congruent. The contribution of larval character states to the reconstruction was limited and less significant because of low weight of most character states.

Relationships among species of subgenus *Elaphrus*

Adults.— The 15 extant species are arranged in five groups. Except for the *marginicollis* group with one species, the remaining four groups are closely related as shown by the incompletely beaded lateral margin of the pronotum. The naturalness of each group, except for the *hypocrita* group, is shown, but relationships between these groups could not be demonstrated (for details see Fig. 177). Adults of the *lheritieri* group are highly differentiated. The three extant species share the following derived character states: explanate lateral margin of pronotum, uniformly dense punctures on pronotum, and oval-shaped main mirror of elytron. The naturalness of the *hypocrita* group could not be shown. However, its two species are similar to one another and may be closely related. The last two species groups are probably closely related, but I failed to find shared derived character states. The *lecontei* group comprises four species having the following derived character states: very dense punctures on proepisternum and on abdominal sterna; abdominal accessory setae less abundant in females. The *riparius* group comprises five closely related species sharing the following derived character state:

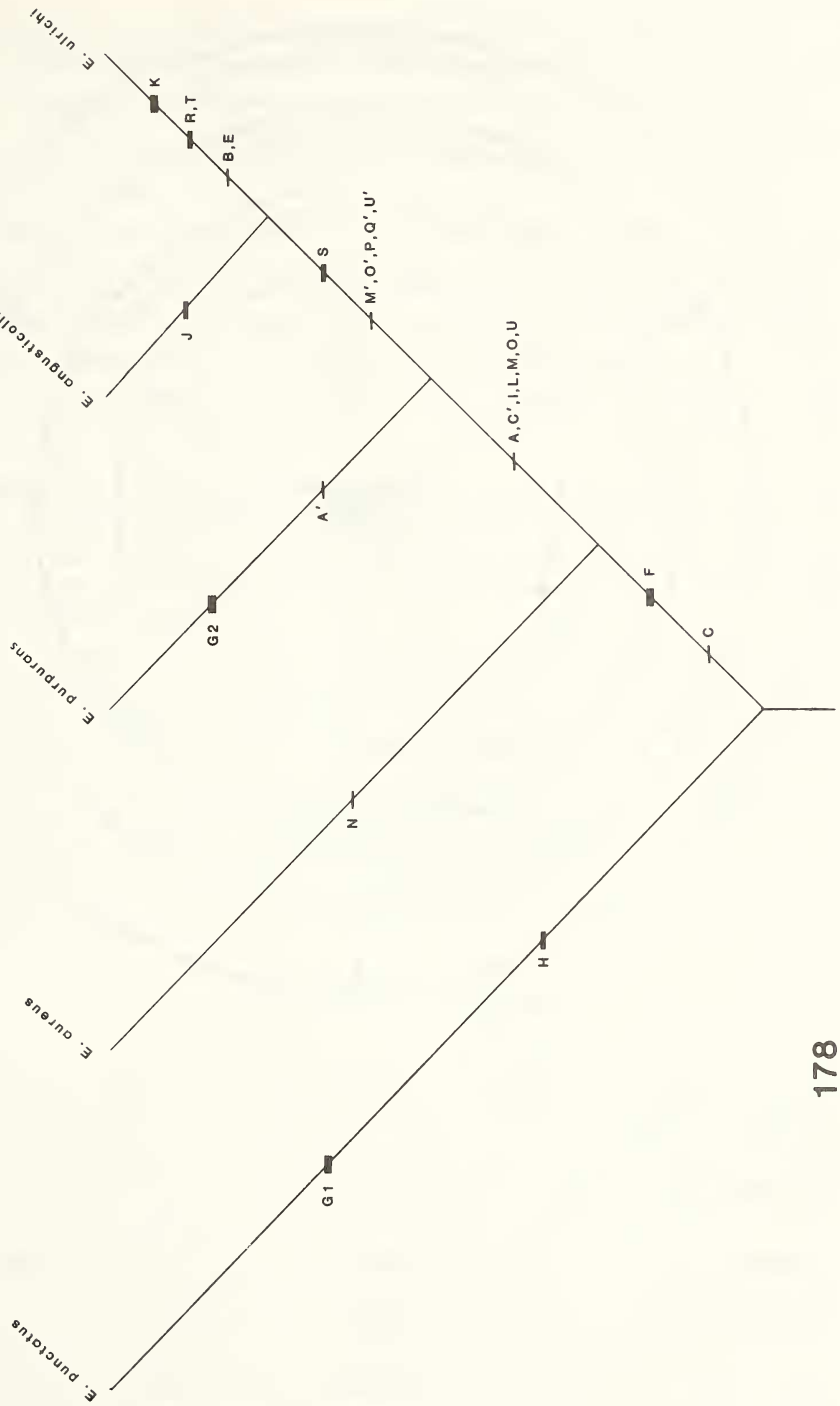


Fig. 178. Reconstructed phylogeny of species of subgenus *Elaphroterus* based on adults and larvae. Capital letters refer to derived states of coded characters (see Tables 58 and 59). Horizontal lines represent an estimated weight of derived character states: one line, low; two lines, medium; three lines high.

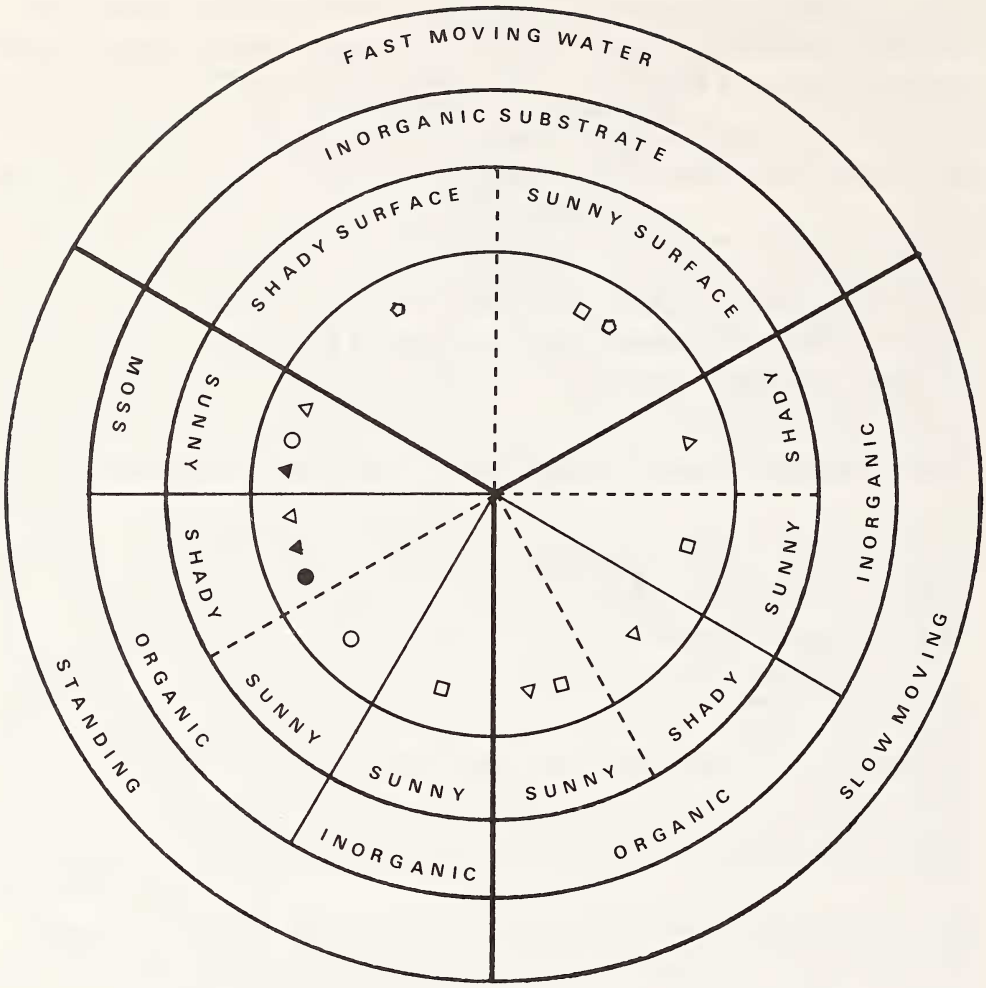


Fig. 179. Correlation diagram for character states of habitat, and circadian activity (diurnal open figures, nocturnal black figures) among species of Elaphrini.

abdominal accessory setae extended to lateral edge of sterna 5 and 6 at least.

In the *lheritieri* group, *E. viridis and E. mimus* are sister species. They share a similar distribution of accessory setae on the dorsal surface, and both have lost pronotal impressions.

In the *lecontei* group, *E. finitimus* and *E. americanus* are almost indistinguishable. Therefore I assume they are sister species. I have no evidence for retracing relationships of *E. californicus* and *E. lecontei.*

In the *riparius* group, there are two pairs of closely related sister species. Firstly, *E. riparius* and *E. tuberculatus* are assumed to be related as they are almost indistinguishable (development of pointed sculpture on abdomen of some adults of *E. tuberculatus* suggest this close relationship). Secondly, *E. parviceps* and *E. tibetanus* are closely related as shown by the few punctures on the abdominal sterna. The position of *E. comatus* is not clear.

Larvae.— As characters were few, and their states of lowest weight, I did not attempt a phylogenetic reconstruction based on larvae.

Relationships among species of subgenus *Elaphroterus*

Adults.— Members of this subgenus are arranged in three groups (Fig. 178). Of these, the *aureus* and *purpurans* groups share the following derived characters: unequal subsutural mirrors; reduced or obliterated lateral margins of pronotum. Relationships among the three species in the *purpurans* group are not clear.

Larvae.— Only larvae of the *aureus* and *purpurans* groups are known. Study of larval characters confirm both groups. Larvae of the single species of the *aureus* group have an unusually short epicranial suture, and those of the three species of the *purpurans* group share the following derived states: smooth inner edge of mandibles of first instars; numerous accessory setae on pronotum and tergal epipleuron of second and third instars. Among the three species of the *purpurans* groups, *E. angusticollis* and *E. ulrichi* are closely related as shown by many derived characters (Fig. 178), although their larvae appear quite dissimilar.

The phylogenies based independently on adults and larvae are congruent and complementary. Using data of both stages, phylogeny of the species of this subgenus was reconstructed (for details see Fig. 178).

CLASSIFICATION OF ELAPHRINI

Classification involves establishment of formal ranks and location of taxa under study within a system of higher taxa. In the phylogenetic system of Hennig (1966), taxa are monophyletic and holophyletic (Ashlock, 1975) and are ranked according to relative age of origin, inferred from distribution of character states. In the so-called "evolutionary" system taxa are monophyletic (holophyletic) or paraphyletic and are ranked according to criteria of divergence, diversity and relative age (Simpson, 1961; Mayr, 1969).

Supra-specific ranks used in this study are four: tribe, genus, subgenus and species group. This number of ranks seems sufficient to encompass the limited diversity and to portray the major features of evolution of the species. The data presented establish that each higher taxon is clearly delimited by uniquely derived character states, and that each of the three groups, currently ranked as a genus, is clearly distinguished from all others. At a higher level this applies to the tribe Elaphrini as currently accepted, and at a lower level to the subgenera of *Elaphrus*. Thus, in recognizing taxa, I have adhered to the principle of monophyly and holophyly of the cladistic system.

I have not felt it necessary or desirable to recognize a formal taxon to include *Blethisa* and *Elaphrus* apart from *Diacheila,* nor to group the subgenera of *Elaphrus,* because of the limted diversity of the Elaphrini.

ZOOGEOGRAPHY OF ELAPHRINI

Introduction

Elaphrine beetles inhabit temperate and boreal zones of the northern hemisphere. To reconstruct the past geographical history of the group, I use working principles presented by Darlington (1957) as reviewed by Erwin (1970). Darlington (1957) presented a list of clues which may help in inferring the probable past history of a group. They are best used in combination, as extinction and recession affect the value of one or more clues.

1. The place of origin may be indicated by the area of greatest diversity. Highly diverse faunas in a given area are probably the result of longer evolutionary history in that area than in other areas where the faunas are little diverse.
2. The place of origin may be indicated by the area of greatest differentiation. Highly differentiated faunas are probably the result of longer evolutionary history in that area than in other areas where the faunas are little divergent.
3. The extent of area probably increases with age of the taxon. The older the taxon, the more geological and paleoenvironmental events would allow it to invade previously inaccessible areas.
4. Present geographic and/or climatic distribution of taxa of older lineages probably indicate the area of origin and/or the probable climatic zone of the common ancestor.
5. The present distribution of vicariant taxa may indicate area of origin and/or the paleoenvironmental events that brought about these vicariant taxa.
6. Fossils may indicate the area of origin and/or the time scale for the reconstruction of past history or the taxa.

I first present evidence gathered from extant and fossil specimens. I then postulate the probable place of origin of elaphrine beetles and retrace the histories of elaphrine genera and sub-genera.

The Evidence

Distribution patterns.— The number of species is nearly equal between the Palaearctic and Nearctic Region for elaphrine genera and *Elaphrus* subgenera *Arctelaphrus* and *Neoelaphrus* (Table 61). However, the subgenus *Elaphrus* is more diverse in the Nearctic Region while *Elaphroterus* is more diverse in the Palaearctic Region. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group is in the Palaearctic, the *fuliginosus* group is in the Nearctic, and the *cupreus* group is about equally represented in Palaearctic and Nearctic Regions.

Within continents, the genera and subgenus *Elaphrus* are most diverse on the Pacific side of both land masses (Table 62). However, the only member of *Arctelaphrus* is Holarctic, the subgenus *Neoelaphrus* is more diverse in Asia and eastern North America, and *Elaphroterus* is more diverse in Europe and western North America.

The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group is more diverse in Asia, the *fuliginosus* group is restricted eastern North America, and the *cupreus* group is more diverse in Asia and western North America.

Table 61. Number of extant species of genus-group taxa of Elaphrini confined to or shared between the Palaearctic and Nearctic Regions.

Taxa	Palaearctic	shared	Nearctic	Total
A. Genera				
Diacheila	3	2	2	3
Blethisa	4	2	6	8
Elaphrus	19	4	19	34
Total	26	8	27	45
B. Subgenera of *Elaphrus*				
Arctelaphrus	1	1	1	1
Neoelaphrus	7	0	6	13
Elaphrus	7	2	10	15
Elaphroterus	4	1	2	5
Total	19	4	19	34
C. Groups of *Neoelaphrus*				
uliginosus	5	0	0	5
fuliginosus	0	0	3	3
cupreus	2	0	3	5
Total	7	0	6	13

Climatic patterns.— In the following discussion, I use broad climatic zones. These zones are briefly defined as follows. The warm temperate zone is characterized by mild winters and long hot summers (in eastern North America this zone extends from southern Pennsylvania to the Gulf of Mexico). The cold temperate zone is characterized by cold winters and hot summers (in eastern North America this zone extends from northern New England to Québec City). The boreal zone is characterized by long cold winters and short cool summers (in eastern North America this zone extends from the Gulf of St. Lawrence to the northern treeline). The northern half of the boreal zone is termed the subarctic zone. The arctic zone is characterized by short cool summers and long, very cold winters.

Species of elaphrines are generally widespread in one or more climatic zones. Elaphrines are found from the southern edge of the tundra to the southern half of the warm temperate zone (Table 63). None is known from subtropical or tropical zones. Adults of most species live at low elevations, but those of a few species are in the subalpine zone. Adults of *Elaphrus* and *Blethisa* are known from the above climatic zones, but those of *Diacheila* are found in the arctic, subarctic or the subalpine zone. Subgenera of *Elaphrus* range in the above climatic zones except for the sole species of *Arctelaphrus*, which is restricted to subarctic and subalpine zones. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group has northern warm temperate, cold temperate and boreal species; the *fuliginosus* group has northern warm temperate and cold temperate species; *the cupreus* group has warm temperate, cold temperate and boreal species.

Diversity in North America.— I present a synopsis for only this continent because it has a varied elaphrine fauna and the distribution patterns are better known to me. However, the general observations presented below are similar for the well collected western Palaearctic

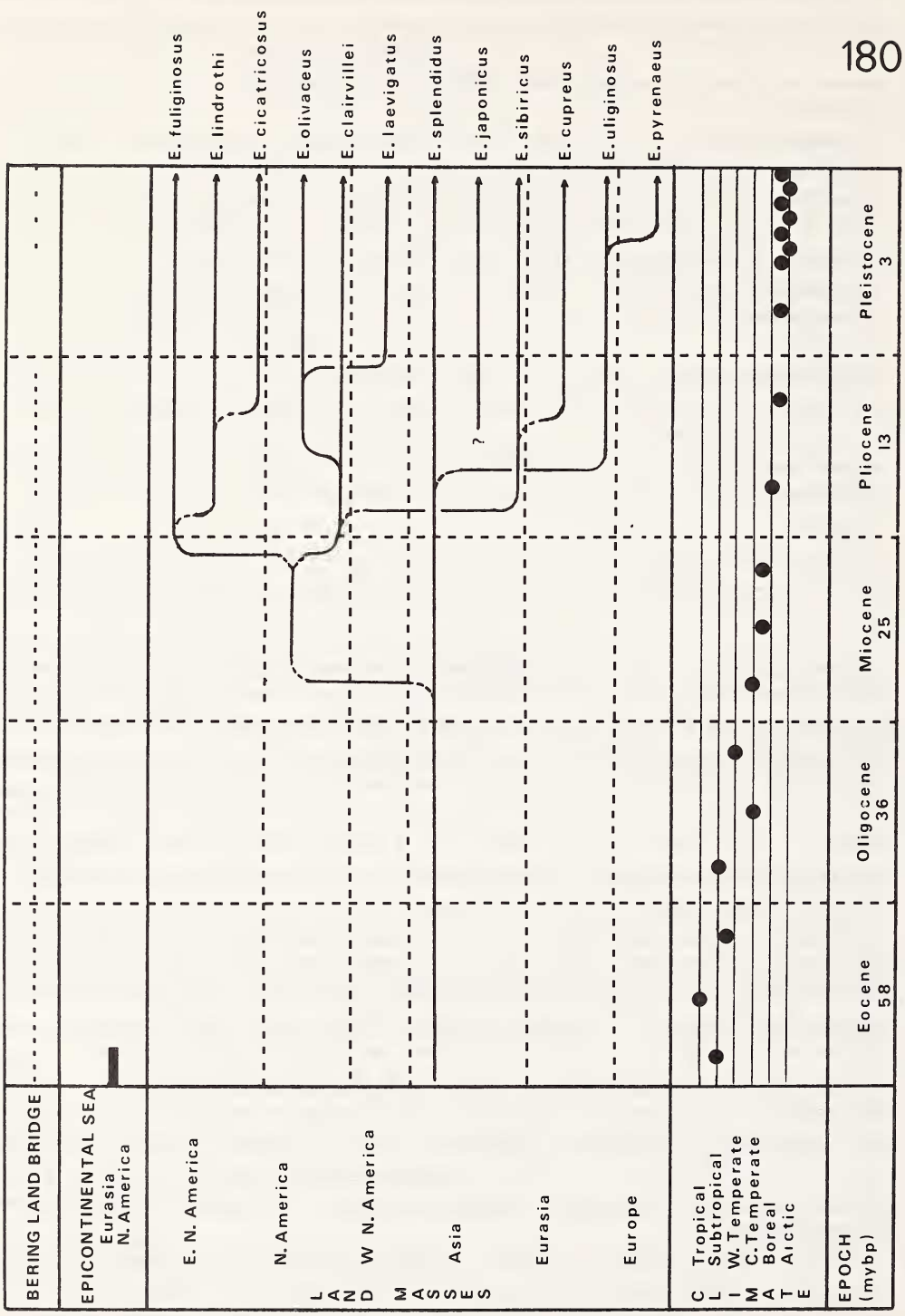

180
E. fuliginosus
E. lindrothi
E. cicatricosus
E. olivaceus
E. clairvillei
E. laevigatus
E. splendidus
E. japonicus
E. sibiricus
E. cupreus
E. uliginosus
E. pyrenaeus
?
BERING LAND BRIDGE
EPICONTINENTAL SEA
Eurasia
N. America
E. N. America
N. America
LAND
W N. America
MASSES
Asia
Eurasia
Europe
CLIMATE
C Tropical
L Subtropical
I W. Temperate
M C. Temperate
A Boreal
T Arctic
E
EPOCH (mybp)
Eocene 58
Oligocene 36
Miocene 25
Pliocene 13
Pleistocene 3

Fig. 180. Summary of probable zoogeographical events during the evolution of subgenus *Neoelaphrus* in Eurasia and North America. Their phyletic position is shown in Fig. 176. Climatic conditions are for Alaska for each period. The North American and Eurasian epicontinental seas are expressed as thick lines and the presence of land bridges as dotted lines in function of time.

Table 62. Number and distribution of extant species of genus-group taxa of Elaphrini within the Palaearctic and nearctic Regions.

Taxa	Palaearctic			Nearctic		
	Europe	shared	Asia	West	shared	East
A. Genera						
Diacheila	2	2	3	2	1	1
Blethisa	1	1	4	6	3	3
Elaphrus	10	6	16	15	7	11
Total	13	9	23	23	11	15
B. Subgenera of *Elaprhus*						
Arctelaphrus	1	1	1	1	1	1
Neoelaphrus	3	2	7	3	2	5
Elaphrus	3	2	6	9	4	5
Elaphroterus	3	1	2	2	0	0
Total	10	6	16	15	7	11
C. Groups of *Neoelaphrus*						
uliginosus	2	1	5	0	0	0
fuliginosus	0	0	0	0	0	3
cupreus	1	1	2	3	2	2
Total	3	2	7	3	2	5

Region. The most notable fact is that diversity is high in all regions between the subarctic and the northern half of the warm temperate zone (excluding the foggy, cool, maritime zones of the Pacific coast and Newfoundland, the subdesert regions, and most of the Canadian Shield) and is followed by an abrupt decrease beyond these climatic zones. In the north around the Mackenzie Delta, adults of seven species are known, but north of the tree line, 70 kilometres away, only two species are known. In Maryland, five species are known, but in Virginia southward, only two are recorded. North of the Mogollon rim in the southwest United States, three species are known, but south of it in the desert area, only one specimen of one species has been collected. In California in the San Francisco vicinity, six species are known, but near Los Angeles, only two are known. Within the area of high diversity, over a surface of about 500 square kilometres, one can expect between five and nine species. Diversity is slightly higher in western North America. The main centres of diversity are: northern California, Yukon, western Northwest Territories, Colorado, and southern Québec.

Dispersal potential.— During their active season on sunny days, adults of *Elaphrus* often fly. Power and frequency of flight is clearly suggested by the abundance of captures of adults of all known New England species near subalpine and alpine bodies of water on Mount Washington, N.H., Mount Mansfield, Vt., and White Face Mountain, N.Y. Although these areas are not normally occupied (*i.e.,* no immatures were found), locality labels, Darlington's observations (pers. comm.) and my own, clearly suggest that such individuals (stragglers) have enough control of their flight to land near suitable habitats.

Habitat diversity.— Data presented here are summarized in Fig. 179. Elaphrine beetles are closely associated with water, except for those of *D. polita.* Adults of *D. arctica* live near

Table 63. Number and distribution of extant species of genus-group taxa of Elaphrini in climatic/geographic zones.

Taxa	Arctic	Boreal	Temperate cold	Temperate warm	Montane
A. Genera					
Diacheila	2	1	0	0	0
Blethisa	1	5	2	2	2
Elaphrus	3	14	19	16	12
Total	6	20	21	18	14
B. Subgenera of *Elaphrus*					
Arctelaphrus	1	1	0	0	0
Neoelaphrus	1	5	8	6	4
Elaphrus	1	5	7	7	5
Elaphroterus	0	3	4	3	3
Total	3	14	19	16	12
C. Groups of *Neoelaphrus*					
uliginosus	0	1	2	1	3
fuliginosus	0	0	2	3	0
cupreus	1	4	4	2	1
Total	1	5	8	6	4

marshes of icy standing water on abundant mosses. Adults of *D. polita* occur under leaf litter, and show many adaptations for digging – probably an early step toward inhabiting subterranean habitats. Specimens of all species of *Blethisa*, except perhaps of *B. eschscholtzi*, are associated with cold standing water. Adults of one species live on thick *Sphagnum* moss carpets, whereas those of other species occur in the shade of dense *Carex* vegetation or on sun-exposed places with open mud and low moss carpets. Adults of *Blethisa* and *Diacheila* are nocturnal, but those of *Elaphrus* are diurnal. Specimens of the sole known species of *Arctelaphrus* live on thick moss carpets. As far as is known, specimens of *Neoelaphrus* occur near rivers or standing water. Individuals of most species live on organic soil, those of *E. lindrothi* are on wet clay flats. The habitat of most species has little or no vegetation, except that of *E. laevigatus* and *E. clairvillei*. Adults of about half of the species are found in sun-exposed areas, but those of others are in deep shade. Specimens of the subgenus *Elaphrus* occur on sun-exposed surfaces. Adults of most species are riparian, but those of a few live near standing water whcih may be cool or warm. Adults of a few species are restricted to beaches with high organic content, but those of most live on sand silt, clay, or a mixture of these soils. Adults of two species are found near alkaline waters. As far as is known, adults of all species of this subgenus are active on low beaches. Adults of *Elaphroterus* are riparian (the habitat of *E. punctatus* is not known). Their preferred habitat may be either sun-exposed or shaded. Specimens of these species, as far as known, live on middle and upper beaches of river banks.

Fossil evidence.— I studied numerous fragments of *Elaphrus* adults of the following species dating from the last glaciation: *E. lapponicus, E. clairvillei, E. olivaceus, E. parviceps, E. americanus* and *E. californicus*. Specimens of these taxa match extant specimens, and those of

E. parviceps and *E. clairvillei* are assigned to extant geographical races. Therefore, there is no evidence of structural changes since the last glacial retreat. These conclusions are backed by Matthews (1974b), Coope (1970) and Lindroth (1969). I also examined excellent fragments of adults of Late Miocene age (between six to ten million years before present–mybp). Some fragments match extant species (*E. lapponicus, E. angusticollis angusticollis),* most extant specimens of *E. riparius* complex (mostly *E. tuberculatus*), one partially present-day adults of *E. sibiricus,* and some extinct species. Matthews (1970, 1974a, 1974b and 1976) observed little or no differentiation among other lowland carabids of the same age and locality.

Synopsis of past geological and climatic events.— North America and Europe were in contact until the end of the Cretaceous (Dietz and Holden, 1970). Early in the Tertiary, Eurasia was linked with North America by Alaska (Hopkins, 1967). The area between eastern Siberia and Alaska is called Beringia.

Epicontinental seas bisected Eurasia and North America in the Late Cretaceous. In North America, a sea extended along a north-south axis east of the Rockies until the end of the Cretaceous (Williams and Stelck, 1975). In Eurasia, a sea extended along a north-south axis east of the Urals until the Early Eocene (Hopkins, 1967). Beringia was probably an exposed land bridge from the Paleocene (63 mybp) until the late Pliocene (3.0 mybp) when a sea transgressed the bridge (Hopkins, 1967; Matthews, 1979). The bridge was reopened only during some of the glacial periods.

The climatic reconstruction is taken mainly from Wolfe (1972) whose study deals with Alaska, a most crucial area. I also have more confidence in his conclusions about past climate, based on his analysis of taxa and leaf physiognomy, than I have in the work of other authors. Climate in the Late Cretaceous and Paleocene was equitable, with subtropical conditions extending into Alaska. Beringia was then as far north as it is today. The temperate zone was probably restricted to northernmost portions of Canada and central Siberia. During the Middle Eocene, Alaska became paratropical. The temperate zone became very restricted or disappeared (Matthews, 1979). From then on, the climate deteriorated until the Pleistocene. During the Late Eocene, the climate of Alaska was equivalent to that of the southern half of the warm temperate zone. During the Early Oligocene, Alaska was subtropical; by Middle Oligocene, it was cold temperate; but in the Lake Oligocene, it was equivalent to that of the northern half of the warm temperate zone. During the Early Miocene, the climate of Alaska was cold temperate; by the Middle and Late Miocene, boreal conditions developed in northern Alaska, while southern Alaska remained cold temperate. During the Pliocene, boreal and subarctic conditions extended over Alaska, and by the Late Pliocene, arctic conditions developed, and along the Bering coast grassland appeared. During the Pleistocene, Alaska alternated between arctic and subarctic conditions.

Climatic Requirements of Ancestors of Major Lineages of Elaphrini

By comparing climatic zones of earlier lineages of species of each higher taxon, one can suggest an hypothesis about the probable climatic tolerance of various ancestors (clue 4). Climatic adaptations of extant species of *Diacheila* suggest a relatively recent subarctic adapted ancestor, those of *Blethisa* a cold temperate or boreal adapted ancestor, the one of *Arctelaphrus* a recent subarctic-adapted ancestor, those of *Neoelaphrus* a warm temperate adapted ancestor, and those of subgenus *Elaphrus* and *Elaphroterus* a cold temperate adapted ancestor.

Center of Origin

I believe that the center of origin of extant genera and subgenera of elaphrines was in the northern Pacific landmass. Evidence is derived from many of the clues presented above. To justify this statement, I first discuss Beringia as a secondary center of radiation in order to establish when elaphrines were there and at what state in their evolution. Then I discuss my reasons for choosing this region as the primary center of radiation.

Beringian Center.— Present diversity of genera and subgenera of elaphrines between North America and Eurasia is the same. Therefore, and earlier corridor-like (Simpson, 1953) bridge must have existed. Diversity and degree of differentiation of genera and subgenera are highest on the Pacific side of the continents. Therefore, it is probable that exchange occurred in that area (clues 1 and 2). Earlier lineages of subgenera suggest that ancestors of *Blethisa* and *Elaphrus* were adapted to the warm or cold temperate zone. Therefore, exchange probably occurred on a bridge with a similar climate (clue 4). The distribution of sister groups among warm temperate *Neoelaphrus* suggests a close association with the mixed mesophytic forest which evolved in northern Asia (clue 5). Finally, Pleistocene and Late Miocene fossils of *Elaphrus* suggest a slow evolutionary rate (clue 6). Therefore, the most probable center of recent infra subgeneric taxa is in northern Asia and/or northwestern North America. Beringia was warm temperate as early as the Middle Oligocene (30 Mybp), and because it was a wide land bridge then, it could have served as a corridor for dispersal of ancestors of *Blethisa* and of *Elaphrus* subgenera *Neoelaphrus, Elaphrus* and *Elaphroterus*. Presence on Beringia of ancestors of extant species of genus *Diacheila* and of *Elaphrus* subgenus *Arctelaphrus,* based on present evidence cannot be confirmed.

Pacific Center.— Since no extant species are adapted to the subtropical zone, the common ancestor of Elaphrini was probably adapted to temperate or colder climates (clue 4). Since genera and subgenera were probably evolved by Oligocene times, the origin of extant elaphrine genera probably goes back to the Late Cretaceous (clues 3 and 6). During the Late Cretaceous cool temperate conditions existed in Alaska (Matthews, 1979), and North America and Eurasia were dissected by north-south epicontinental seas. Therefore, exchange between Asia and Europe, or between western North America and eastern North America was minimal. If the center of origin was on the Atlantic side of both continents, much exchange would have occurred between Europe and eastern North America as both continents were still broadly connected. Moreover, elaphrines would show a similar distribution and differentiation pattern to that of the Ansiodactylina (Noonan, 1973) which are most diverse on the Atlantic side of the continents. Therefore, a northern Pacific center is more compatible with the evidence. This distribution is also more compatible with the probable center of evolution of its Asiatic sister groups, the tropically-adapted Melaenini and mountain-adapted Broscina. By Eocene times, ancestors of many elaphrine lineages may have been segregated in restricted and isolated temperate enclaves in Siberia and Beringia along the Arctic coast.

Evolution of Habitat Preferences among Elaphrine Genera and Subgenera

As all elaphrines, except adults of *D. polita,* are associated with wet environments, the immediate ancestor of elaphrines most probably was associated with wet soils. I postulate that this ancestor was nocturnal (as adults of less derived *Blethisa* and *Diacheila* are nocturnal or crepuscular) and lived near standing water among moderately short vegetation. This habitat matches quite closely that of *D. arctica* and most extant species of *Blethisa* (clue 4). The main evolutionary step was taken by the immediate ancestor of *Elaphrus* as it became a diurnal

predator on open surfaces with little vegetation to obscure vision. Eyes of adults of *Elaphrus* are indeed large with wider angle of vision and more numerous omatidia and those of *Diacheila* and *Blethisa*. The cellular arrangement is of photopic type (Kuster, 1979). Since adults of many species belonging to older lineages of *Elaphrus* are associated with moss carpets, the ancestor may have been adapted to such habitats. The single species of *Arctelaphrus* is found in a habitat similar to that postulated for the ancestor.

The habitat of species of earlier lineages of *Neoelaphrus* fits the above description (*E. uliginosus,* and *E. pyrenaeus)*. However, younger lineages of *Neoelaphrus* invaded shaded habitats (*E. cupreus, E. lindrothi, E. clairvillei,* and *E. laevigatus*). Species of the *fuliginosus* group are partly riparian, and those of the *cupreus* group have riparian species (the *cupreus* subgroup) and standing water species (the *clairvillei* subgroup). Adaptation to standing water habitats is considered secondary as these became available again after evolution of the more cold hardy elements of the *cupreus* group.

The common ancestor or species of subgenera *Elaphrus* and *Elaphroterus* became adapted to substrates low in organic matter. The ancestor of species of subgenus *Elaphrus* remained adapted to the wet habitats, and invaded different and finer substrates. The ancestors of species of *Elaphroterus* became adapted to habitats near moving waters and to the moist section of beaches.

Past History of Elaphrini

Based on the median lobe of males, Elaphrini are probably related to Broscina and Melaenini. The relationships of elaphrines with each of above groups is not clear. The Broscina are diverse in mountains of warm temperate and subtropical Asia, and the extant Melaenini in African and Asian tropics. Thus, the elaphrine ancestor might have been subtropical. Since elaphrines are not found near subtropical regions, the immediate elaphrine ancestor probably evolved in Late Cretaceous and survived in warm-temperate areas where it became diverse and gave rise to ancestors of extant genera and subgenera. The temperate adaptation of elaphrines and their absence from the subtropical areas where the common ancestor probably evolved might best be explained by the taxon cycle theory (Wilson, 1961).

Wilson's taxon cycle can be briefly summarized as follows. Invaders from zones of high diversity (larger land masses in Wilson) establish themselves in a zone of lower diversity (smaller and younger islands in Wilson) and become ecologically released (islands, in Wilson, are younger and support unbalanced faunas, and as a consequence, new comers are likely to increase ecological amplitude). These invaders evolve and, in turn, may be displaced by more recent invaders from regions of high diversity (new invasion from larger and older land masses in Wilson) and adapt to new niches with lower diversity (mountain forests in Wilson) or, they may become extinct, or they may colonize and survive in a new zone (another island of similar or smaller size in Wilson) with similar or lower diversity. However, the descendants of the first invader are unlikely to invade an area of intensive competition pressures successfully (larger and older land masses in Wilson). Darlington (1943) alluded to this cycle (origin of shortwing species of mountain carabids), clearly referred to it later on (1957), and presented evidence based on phylogenetic data (1971). Erwin (1979) referred to this cycle and suggested a new name "Taxon Pulse", and stressed that evolutionary changes were generally in one direction (*i.e.,* toward extinction), and that speciation events are likely to be triggered by succeeding waves of invaders. Islands are not only geographical but ecological entities. They are generally areas with lower diversity and consequently of less intensive competition pressures (*i.e.,* an

island with unbalanced fauna, a recently formed life zone like the arctic region, a habitat with many open niches like a peat bog). Therefore, the important factor in orienting this cycle is the difference in diversity between climatic zones (altitudinal or latitudinal), land masses, or habitats. An interesting characteristic of areas with lower diversity is the unexpectedly high proportion of eurytopic species. Moreover, I do not feel that invaders should be generalists (Wilson, 1961; Darlington, 1971; Erwin, 1979), or land size important in giving rise to these cycles. Invaders in proximity of zones to invade may be specialized, but at least they are pre-adapted to cross a special barrier (water or mountain gaps, cold winters, different climatic regimes, special habitats). Land size ultimately affects diversity (Darlington, 1943), but is not always related to it (arctic regions are immense and yet very low in diversity).

I feel this theory can account for extinction of groups in regions or life zones of origin, and for their presence in younger regions or life zones than that of the lineage studied. Thus, the restricted and young temperate zone in Late Cretaceous may have been a zone of low diversity in which elaphrine radiation started. This theory has been used in studies of historical reconstruction of some groups of ground beetles (Allen and Ball, 1979; Erwin, 1979).

Present ranges of *Diacheila* species are along the tundra-treeline boundary. Degree of divergence and fossils studied (Pleistocene and Miocene samples) clearly suggest an origin older than the present arctic regions (estimated to be about 6 million years old). Marsh adaptations are not evolved in mountain regions (personal observations based on North American carabid fauna) but rather in lowlands. Their evolutionary history probably started in lowland marshy regions under milder climatic conditions. Extant species, as far as studied, are associated with habitats of low insect diversity, especially ground beetles. These habitats are probably places of low competition pressures for these beetles.

The history of species of *Diacheila* might be presented as follows. Early in the history of this genus, there might have been a radiation, as suggested by marked divergence between extant species. Perhaps many species became extinct following radiation of more successful competitors. A few descendant species survived, probably in a more recently evolved life zone (further north) either in marshy environments or more specialized niches. This cycle of extinction and/or displacement continued until tundra-adapted species evolved. The range of species of *Diacheila* may have extended in Pliocene time across Beringia, but I suspect Holarctic ranges were achieved in the Pleistocene during glacial periods after the ancestors of two extant species became adapted to tundra.

Present species of *Blethisa* are structurally divergent. Evolutionary rates, indicated by fossils of Late Miocene times, are slow. Therefore, the age of the immediate ancestor may be older than the boreal zone where most species are found today. The common ancestor may have originated during the late Cretaceous. Their infrequent presence in cold temperate regions suggests that extinction of ancestral descendants occurred in the temperate zone. However, in the boreal zone, a younger region with lower competition pressures, a few descendant lineages survived and even radiated. In time, new invaders established themselves in boreal regions and probably brought to extinction many species except for a few adapted to marshy environments of tundra-treeline boundary regions or marshes with low diversity (short *Carex* and *Sphagnum* bogs). Two extant species are Holarctic, one, a boreal species, probably invaded the Nearctic during the Pliocene, and another, an arctic species, spread across Beringia during the Pleistocene.

Miocene fossils of *Elaphrus* studied (at least adults of five species representing all subgenera) clearly suggest slow evolutionary rates. The structural divergence between most

species is marked. The past history of some species in some subgenera is more complex than suggested in present distribution patterns.

The oldest lineage is represented by one surviving species in the subgenus *Arctelaphrus* . This is a subarctic species. Since Pleistocene and Miocene fossils of this species show no sign of structural changes, I feel the history of species of this subgenus is much older than the subarctic zone. Thus, its ancestor probably evolved under milder climates. Today the absence of any species further south may suggest extinction of most descendants of the *Arctelaphrus* ancestor, possibly due to higher competition pressures in older and warmer regions or habitats. Present-day populations of *E. lapponicus* are found in a habitat of low diversity, especially of carabid beetles. During the Pleistocene, *E. lapponicus* became Holarctic and probably invaded Kodiak Island in the Late Pleistocene giving rise under repeated harsh glacial conditions of the refugium to *E. lapponicus obliteratus.*

The complex past history of the species of *Neoelaphrus* presented below is summarized in Fig. 180. From the Late Eocene on, the temperate zone enlarged as the climate cooled. Therefore, in early Tertiary the ancestor of *Neoelaphrus* probably spread over wider areas in an evolving warm temperate forest. By the Late Oligocene (25 mybp), the range of this ancestor extended over Berginia. Climatic conditions continued to deteriorate, and by the Middle Miocene (17 mybp) as Beringia was becoming boreal, the ancestral population previously adapted to warmer conditions became divided. The Siberian stock gave rise to the ancestor of the *uliginosus* group while the North American stock gave rise to the common ancestor of the *fuliginosus* and *cupreus* groups.

Since no extant species of the *uliginosus* group are known in North America, it is probable that the boreal adaptations shown by *E. splendidus* are recent and not earlier than Late Pliocene. Events conducive to evolution of the extant species of this group cannot be interpreted in terms of the known distributions of extant species and past geological events. The *E. uliginosus* ancestor evolved in Europe, and, during glacial phases of the Pleistocene, extended toward southern France, leaving a subalpine stock that gave rise to *E. pyranoeus. E. uliginosus* seems to have been preadapted for invading mountains as suggested by the Apennine, Balkan and Tien-shan mountain populations. Of extant species, *E. splendidus* and *E. japonicus* belong to the oldest lineage. *E. japonicus* is closely associated with the mixed mesophytic forest (perhaps the ancestral habitat), and *E. splendidus* with cold temperate and boreal forests (perhaps a recent adaptation).

The North American stock of *Neoelaphrus* gave rise to the extant species of the *fuliginosus* group that is closely associated with the mixed mesophytic forest (perhaps the ancestral habitat). Distribution of present species, and geological or climatic events cannot account for their speciation. The amount of divergence achieved suggests that the *fuliginosus* group evolved quite early in Late Miocene or Early Pliocene and that speciation probably occurred somewhere in Canada where the mixed mesophytic forest was widespread.

The North American stock of *Neoelaphrus* also gave rise to the ancestor of the *cupreus* group. In time, a successful stock, adapted to cold temperate and boreal regions, evolved. This adaptation allowed the common ancestor to spread northward and across Beringia as early as the Middle Miocene (13 mybp). Thereafter, cooler conditions over Beringia effectively isolated the ancestor of the *cupreus* group into two stocks. The Asiatic stock became the ancestor of the *sibiricus* subgroup that gave rise to *E. cupreus* and *E. sibiricus.* The event conducive to this speciation process is unknown, since the extant ranges overlap extensively in Asia. The North American stock gave rise to the *clairvillei* subgroup adapted to standing water. This stock gave

rise to the boreal-adapted ancestor of *E. clairvillei* and to the common ancestor of *E. olivaceus* and *E. laevigatus*. Events leading to formation of these two ancestors are unknown. The common ancestor of *E. olivaceus* and *E. laevigatus* was probably widespread across the continent. However, following development in Pliocene time of colder conditions, the ancestral population could have become divided by cold temperate grassland and drier zones in the region of the Great Basin. The stock west of the Cascades gave rise to *E. laevigatus* and the eastern stock gave rise to *E. olivaceus*.

A phylogenetic reconstruction of extant members of the subgenus *Elaphrus* could only be attempted partially. However, enough information is available to suggest a taxon cycle in action north and south as well as a reversal of the cycle. The habitat and structural differentiation is great in this subgenus. Some species are widespread and in process of radiation (*E. californicus, E. finitimus, E. americanus, E. tuberculatus* and *E. riparius*). These species are successful in a wide range of latitudinal and altitudinal zones and belong to the two most highly evolved species groups. Some species show what is probably a taxon cycle in reverse (*E. finitimus* and *E. lecontei*) as some of their populations are successfully invading zones of high diversity farther south. The groups which evolved earlier (*marginicollis, lheritieri* and *hypocrita* groups) have species with restricted distributions. Despite the extreme southerly range of members of the *lheritieri* group, these species survive in habitats of low diversity. Their pattern does not represent a reversal of the taxon cycle, but rather the contrary. Both species of the *hypocrita* group are found in the warm temperate zone and their success seems moderate judging by their narrow latitudinal range. The ancestors of the *marginicollis, lheritieri* and *hypocrita* groups were probably widespread in warm temperate regions of the Palaearctic and the Nearctic region. The present disjunct disbribution is probably relictual. On the other hand ancestors of the *lecontei* and *riparius* groups may have been separated into Palaearctic and Nearctic stock populations during the Early Miocene. The Nearctic stock evolved and gave rise to extant members of the *lecontei* group. The speciation events cannot be traced. Meanwhile those of the Palaearctic stock gave rise to present species of the *riparius* group whose speciation events cannot be traced also. However, during the Pleistocene, the most cold-adapted species (*E. tuberculatus* and *E. parviceps*) extended their ranges across Beringia into the Nearctic region during glacial events.

The ancestor of *Elaphroterus* was probably associated with fast moving waters of mountain origin. It probably invaded this unusual habitat from the Asiatic center of origin when much of the Asiatic mountain ranges were well formed. Species of oldest lineages (*E. punctatus* and *E. aureus*) are from the cold temperate zone. From the *E. aureus* ancestor, the ancestor of the *purpurans* group evolved. This ancestor spread to, or was in, Beringia by the Middle Miocene, but cold conditions during the late Miocene divided the ancestral stock. The nearctic stock gave rise to extant *E. purpurans*. The Palaearctic stock gave rise to the common ancestor of *E. ulrichi* and *E. angusticollis*. This last species spread and divided into eastern and western Palaearctic populations which gave rise to two subspecies. The eastern Palaearctic subspecies invaded the western Nearctic region during the Late Pleistocene.

Conclusion

Beringia was a most important area during the formation of the flora (Wolfe, 1972) and fauna (Simpson, 1953) of the Palaearctic and Nearctic region. This bridge was in existence during most of the Cenozoic period. The main floral and faunal source areas during the first half of this period were either in tropical or temperate Asia (Wolfe, 1972). In Late Tertiary,

North America served also as a source area (Wolfe, 1972; Simpson, 1953). Beringia served mostly as a corridor or filter route for plants and animals adapted to climatic conditions of the bridge. From the Paleocene until the Oligocene, subtropical and paratropical conditions in Alaska allowed tropical Asiatic elements to invade North America. Among carabids I do not know of taxa that use this early route. From the Middle Oligocene until the Early Miocene, numerous temperate Asiatic elements extended into North America. This exchange was extensive, as today numerous extant genera and subgenera are still shared. The following carabid genera used this route then: *Loricera* (Ball and Erwin, 1969), *Badister, Diplocheila,* and *Dicaelus* (Ball, 1959), *Calathus* (Ball and Nère, 1972) and *Dicheirus* (Noonan, 1975). During the Late Miocene and the early Pliocene, boreal elements from both continents were exchanged. These elements were derived mostly from temperate counterparts on each continent. Finally, Beringia was the seat of exchange of subarctic and arctic elements during glacial phases of the Pleistocene as suggested by numerous holarctic species of plants and animals shared today (Hultén, 1968; Lindroth, 1961; Ball, 1966) and confirmed by unchanged Pleistocene fossils observed by Lindroth (1969), Coope, (1970) Matthews (1970, 1974a and 1974b) and myself.

In summary, ancestral and extant members of *Elaphrus* crossed Beringia several times. The sole member of *Arctelaphrus* invaded North America during one of the glacial periods of the Pleistocene. In *Neoelaphrus,* one early invasion from Asia occurred in the Late Oligocene followed by another in the Middle Miocene from North America. In *Elaphrus,* one invasion from North America in the Early Miocene by one or two ancestral species was followed by invasion into North America by two Palaearctic descendants during a glacial period of the Pleistocene. In *Elaphroterus,* one stock invaded North America in the Middle Miocene and another during one of the glacial periods of the Pleistocene.

The ancestral habitat of *Elaphrus* consists of sun-exposed, moist or wet, and open surfaces which are without, with scattered, or dense and short vegetation. This type of habitat is common to adults of some species (usually early lineages) in all subgenera except those of *Elaphroterus.* From this type of habitat, shifts took place in many directions (Fig. 179). In species of *Neoelaphrus,* there were shifts to shaded surfaces (*E. japonicus, E, cupreus, E. cicatricosus, E. lindrothi, E. clairvillei* and *E. laevigatus),* to slow moving waters (*E. cupreus, E. cicatricosus* and *E. lindrothi),* and to inorganic substrates (*E. lindrothi).* In species of *Elaphrus,* there were shifts to slow moving waters (*E. ruscarius, E. californicus, E. americanus, E. finitimus, E. riparius* and *E. tuberculatus*), to inorganic substrates (*E. ruscarius, E. californicus, E. lecontei, E. americanus sylvanus, E. finitimus, E. riparius, E. tuberculatus* and *E. parviceps*), and to saline substrates (*E. lecontei* and *E. lheritieri*). In species of *Elaphroterus,* there were shifts to fast moving waters (all species), to upper beach (all species), and to shaded surfaces (*E. purpurans* and *E. angusticollis longicollis*).

The postulated complex history of elaphrines, with exchanges between continents and distributional changes is best interpreted considering geological and climatic events, but radiations and extant distribution patterns are perhaps best suggested by Wilson's (1961) principle of taxon cycle. The potential of Wilson's theory in biogeography is more concretely illustrated by Wolfe's (1972) study of the origin of the mixed mesophytic and northern hardwood forests. Most elements of these forests originated in older and larger areas with high diversity (farther south), followed by various degrees of radiation in new or younger life zones, but rarely followed by a reciprocal invasion and radiation from northern areas into the more diverse southern communities. I feel students of biogeography of temperate, boreal and arctic

faunas and floras would have much to gain in considering Wilson's theory following an analysis of taxa distribution and their reconstructed phylogeny. Many insects are closely associated with floras similar to those studied by Wolfe, and the pattern suggested by these floras is likely to be similar in those insects. The theory of taxon cycles may have wide application in studies of northern biographraphy.

CONCLUDING REMARKS

What is the future in studies of *Elaphrus*? Systematic and taxonomic problems in need of studies have been outlined along the text and in related publications. Since species of *Elaphrus* are in a mature level of taxonomic and systematic understanding, students in other fields of biological sciences may look upon them as subjects for investigation. Bauer (1973, 1974 and 1976) studied many aspects of the ecology and ethology of species of his region. Some species are stenotopic and others eurytopic, yet we do not know about the stimuli that orient adults to their specific macro- and micro-habitat. The numerous species of *Elaphrus* are likely to be a gold mine of challenges for comparative ethological studies. Firstly, adults are exceptionally easy to observe. Adults of all species are diurnal, active during best weather conditions, and exhibit an exceptionally long period (three to six months) of activity and reproduction, those of most species are on surfaces almost free of vegetation and rough organic debris, and those of many species are restricted narrowly laid habitats. Secondly, there is a wide range of behavior patterns associated with cryptic coloration (displacement, mating, hunting for mates and food, grooming, etc), with type of water in proximity (river or marsh), and with acute sight (mating, hunting for food and mates, enemies etc.).

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INDEX TO NAMES OF TAXA
(Synonyms in italics)